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The ecology of early juvenile *Nucella emarginata* (Gastropoda, Prosobranchia): Are hatchling snails simply small adults?

BY

©

LOUIS ANDRÉ GOSSELIN

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

DEPARTMENT OF BIOLOGICAL SCIENCES

Edmonton, Alberta

Fall 1994

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Abstract

Our current understanding of the mechanisms regulating marine intertidal populations and communities are almost exclusively based on studies of larvae and adults. Details of the ecology of the early juvenile period, however, are sparse and the effect of events occurring during this period on population distribution and abundance remains unclear. If early juveniles, which are often morphologically similar to adults except for size, are also ecologically similar to adults, then one would only have to study the adults to identify the mechanisms regulating their distribution and abundance throughout independent benthic life. In terms of their ecology, early juveniles would in essence be small adults. But is this the case?

To address this question, I studied the ecology of early juvenile *Nucella emarginata*, an intertidal predatory snail. Newly hatched *N. emarginata* were smaller than adults by more than three orders of magnitude, had little information and experience regarding their new environment, and were considerably more vulnerable than adults to desiccation. Hatchlings and adults were consumed by different sets of predators, and differed in feeding habits, in microhabitat use, and in shell coloration. These differences constitute important ontogenetic changes in the relationship of the organism with its environment. Hence, the early juvenile period is ecologically distinct from the adult period.

The timing of ontogenetic changes was then examined to define the transition marking the end of the early juvenile stage, and thus establish the duration of the early juvenile stage in *N. emarginata*. Vulnerability to mortality factors, distribution, and the colour of the shell remained homogeneous up to ≈3 mm shell length. Snails then became increasingly capable of withstanding direct exposure to low tide desiccation conditions, and vulnerability to hatchling predators decreased to very low levels as snails grew from 3 - 7 mm shell length. The gradual release from the restrictions imposed by desiccation and predation corresponded to an increased frequency of occurrence on open surfaces and a shift in shell colour. The early juvenile stage in *N. emarginata* therefore lasts from the moment they emerge from their egg capsule until they reach ≈3 mm shell length. The snails then undergo a discrete ecological transition between the sizes of 3 - 7 mm.

The information presently available for other benthic species suggests that the early juvenile period may also be an ecologically distinct stage in many marine macrobenthic species with motile juveniles. In such species, a comprehensive knowledge of the mechanisms regulating their populations will not be possible until the ecology of the early juvenile stage has been elucidated. The study of early juvenile ecology will also provide essential information for understanding life history strategies.

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The ecology of early juvenile *Nucella emarginata* (Gastropoda, Prosobranchia):
Are hatchling snails simply small adults?

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CHAPTER I

General introduction:
The early juvenile ecology of intertidal invertebrates

Significance of ecologically distinct stages of life

Innumerable studies over the last century have provided substantial insight into the factors that regulate marine benthic populations and communities by examining the relationships between intertidal organisms and the biotic and abiotic components of their environment (cf. reviews by Connell, 1972; Paine, 1977; Underwood, 1979). These studies, however, mainly focused on adult or late juvenile individuals, and little attention was paid to the early life history. As more information was acquired, it became increasingly clear that events occurring during the adult stage often had a limited impact on population and community structure. Renewed interest in larval ecology then yielded considerable advances in understanding recruitment and life history strategies (Strathmann, 1985; Rumrill, 1990), and quantitative experimental studies of the larval stage have increased our understanding of how benthic populations are regulated (Connell, 1985; Underwood and Fairweather, 1989; Gaines and Bertness, 1993). Knowledge of the ecology of benthic organisms during the larval period is essential because larvae are ecologically distinct from adults: their requirements, mortality factors, distribution, and behaviour differs from that of adults of the same species. Thus, even if the interactions that were important to the adult were thoroughly understood, this information would not be relevant to the larva. Since our understanding of benthic populations and communities has increased as a result of studying larvae as a separate stage, it is necessary to ask whether all ecologically distinct life stages have been identified. A comprehensive knowledge of the mechanisms regulating benthic populations will not be possible until the ecology of every stage has been elucidated.

The early juvenile period

One period of life rarely examined in benthic marine invertebrates is the early juvenile period. Yet, over 98% of benthic marine invertebrates may die during the juvenile period (Thorson, 1966; Spight, 1975), and settlement and early post settlement, rather than larval life, may actually be the time of greatest mortality (Jablonski and Lutz, 1983). Factors that influence the survival of individuals during the early juvenile period can therefore have a considerable effect on recruitment to the adult population (Strathmann, 1975; Sarver, 1979; Rowley, 1989; Brawley and Johnson, 1991; Gosselin and Qian, submitted). In view of this, it is surprising that the field of juvenile ecology is still virtually unexplored.

At present, the early juvenile period has been studied more in lobsters than in other subtidal benthic invertebrates (*Homarus americanus*: Lawton, 1987; Lavalli and Bardshaw, 1989; Wahle, 1992; Wahle and Steneck, 1992; *Panulirus argus*: Herrnkind and Butler, 1986; Smith and Herrnkind, 1992), undoubtedly as a result of the commercial interest of these species. Most of these studies have focused on microhabitat selection and on the significance of microhabitat use. Information regarding the early juvenile ecology of intertidal organisms, however, is limited and has mostly been obtained from studies of sessile organisms such as barnacles (Foster, 1971; Denley & Underwood, 1979; Connell, 1985; Miller & Carefoot, 1989) and recently macroalgae (Vadas et al., 1990; Brawley and Johnson, 1991). In addition, most information on early juvenile benthic invertebrates is either reported as part of a broader study focusing mainly on adults (Frank, 1965; Connell, 1961, 1970; Branch, 1975), or as laboratory studies of a specific interaction of the individual with one component of the environment, such as the importance of body size on the outcome of predator-prey interactions (Palmer, 1990), or the influence of exposure to specific odours during larval development on chemoattraction (Williams et al., 1983; Rittschof and Brown, 1986). Few studies have attempted to characterize the benthic environment as perceived by early juvenile organisms. Moreover, there have been no attempts to achieve a comprehensive understanding of the ecology of early juvenile invertebrates in the field. Such a synthesis is necessary to assess the rôle of the early juvenile period in determining population dynamics and community structure, and to understand the significance of life history strategies. To achieve this requires that the main mortality factors and essential resources critical to early juveniles be identified, as well as the behavioural, structural, and physiological adaptations that are necessary to survive though this period of extreme vulnerability. Although the task is formidable and could not possibly be completed in a single thesis, the present study nevertheless adopts this approach with the intent of providing a first synthetic view of life during the early juvenile period in intertidal invertebrates and providing suggestions for future directions in research.

Why study intertidal snails?

Early juvenile snails are among the easiest juvenile invertebrates to collect and study owing to the presence of an external shell. Many intertidal snails offer the additional advantages of being abundant and accessible. Newly hatched *Nucella emarginata* (Deshayes) (northern) (cf. Palmer et al., 1990), an intertidal prosobranch gastropod, are particularly amenable to the study of early juvenile ecology. *Nucella emarginata* has a broad geographic range along the Pacific coast of North America (Palmer, 1984, 1985) and is often one of the most abundant gastropod species inhabiting rocky shores. Complete larval development occurs within benthic egg capsules, and individuals emerge as crawl-away juveniles. Due to an extended spawning season, hatchlings are available in the field for at least 3 to 7 months of the year (Spight, 1982; appendix 2). Newly hatched *N. emarginata* are relatively undisturbed by gentle handling (Gosselin, 1993) and will readily feed, grow, and survive to maturity under laboratory conditions (Palmer, 1985; Gosselin, 1993). However, due to their small size, high surface to volume ratio, and fragile bodies, early juvenile snails may be highly vulnerable to factors such as desiccation, high temperatures, mechanical damage, and predation (Branch, 1975; Underwood, 1979). Furthermore, early juveniles are generally much more difficult to locate in the field than adults. The logistical and technical research problems resulting from the above features are undoubtedly some of the reasons why so few studies have examined this period of life in snails or in other marine invertebrates. However, these same features suggest that early juveniles are unlikely to interact with their environment in the same way as the adults. If this is the case, the rewards of studying early juveniles will far outweigh the efforts and difficulties that are involved.

Objectives of the thesis

The general goals of this thesis are to: 1) identify the main requirements and factors of mortality of early juveniles of the intertidal gastropod, *Nucella emarginata*; 2) describe adaptations that significantly reduce their susceptibility to factors of mortality; and 3) compare the ecology of hatchlings and adults to determine if hatchlings can simply be considered as small, non-reproducing adults, or whether the early juvenile period is an ecologically distinct stage of the animal's life.

The present study was conducted at the Bamfield Marine Station and at nearby field sites in Barkley Sound, on the west coast of Vancouver Island, British Columbia, Canada.

Content of the thesis

Food requirements and mortality factors

Chapter II examines the onset of feeding in newly hatched *N. emarginata* and describes the food sources they can use. Chapter III identifies the biotic and abiotic factors to which hatchlings are most vulnerable, and which are likely to constitute the most important selective pressures during the early juvenile period.

Adaptive traits

Chapter IV identifies the microhabitats used by hatchling *N. emarginata* in the field and examines the significance of habitat use in terms of protection from mortality factors and availability of prey. In chapter V, the prey preferences of hatchlings are determined and the significance of these preferences is examined in terms of the energy maximization premise and an alternate hypothesis that the preferred prey are used as cues to locate protective microhabitats.

Conclusion: Are hatchling snails simply small adults?

In chapter VI, I review the data presented in chapters II to V and compare these with information on the ecology of adult *N. emarginata* to determine if the early juvenile period is ecologically distinct from the adult period. I then examine the timing of ontogenetic changes in susceptibility to mortality factors, distribution among microhabitats, and shell coloration to identify the transition period between early juvenile and late juvenile/adult.

The following chapters have been written in paper format. Some repetition of text and references was necessary to ensure that each chapter constitute a self-contained document that could be read independently from the rest of the thesis.

References

Branch, G.M. 1975. Ecology of *Patella* species from the Cape Peninsula, South Africa. IV. Desiccation. Mar. Biol. 32: 179-188.

Brawley, S.H. and L.E. Johnson. 1991. Survival of fucoid embryos in the intertidal zone depends on developmental stage and microhabitat. J. Phycol. 27: 179-186.

Connell, J.H. 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. Ecol. Monogr. 31: 61-104.

Connell, J.H. 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. Ecol. Monogr. 40: 49-78.

Connell, J.H. 1972. Community interactions on marine rocky intertidal shores. Ann. Rev. Ecol. Syst. 3: 169-192.

Connell, J.H. 1985. The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. J. Exp. Mar. Biol. Ecol. 93: 11-45.

Denley, E.J. and A.J. Underwood. 1979. Experiments on factors influencing settlement, survival, and growth of two species of barnacles in New South Wales. J. Exp. Mar. Biol. Ecol. 36: 269-293.

Foster, B.A. 1971. Desiccation as a factor in the intertidal zonation of barnacles. Mar. Biol. 8: 12-29.

Frank, P.W. 1965. The biodemography of an intertidal snail population. Ecology. 46: 831-844.

Gaines, S.D. and M.D. Bertness. 1993. The dynamics of juvenile dispersal: why field ecologists must integrate. Ecology. 74: 2430-2435.

Gosselin, L.A., 1993. A method for marking small juvenile gastropods. J. Mar. Biol. Ass. 73:963-969

Gosselin, L.A. and P.-Y. Qian. Submitted. Early postsettlement mortality of intertidal barnacles: a critical period for survival. (Ecology)

Herrnkind, W.F. and M.J. Butler, IV. 1986. Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobsters, *Panulirus argus*. Mar. Ecol. Prog. Ser. 34: 23-30.

Jablonski, D., & R.A. Lutz. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. Biol. Rev. 58: 21-89.

Lavalli, K.L. and D.E. Barshaw. 1989. Post-larval American lobsters (*Homarus americanus*) living in burrows may be suspension feeding. Mar. Behav. Physiol. 15: 255-264.

Lawton, P. 1987. Diel activity and foraging behavior of juvenile American lobsters, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 44: 1195-1205.

Miller, K.M. & T.H. Carefoot. 1989. The role of spatial and size refuges in the interaction between juvenile barnacles and grazing limpets. J. Exp. Mar. Biol. Ecol. 134: 157-174.

Paine, R.T. 1977. Controlled manipulations in the marine intertidal zone, and their contributions to ecological theory. Acad. Nat. Sci. Spec. Publ. 12: 245-270.

Palmer, A.R. 1984. Species cohesiveness and genetic control of shell colour and form in *Thais emarginata* (Prosobranchia, Muricacea); preliminary results. Malacologia 25: 477-491.

Palmer, A.R. 1985. Genetic basis of shell variation in *Thais emarginata* (Prosobranchia, Muricacea). I. Banding in populations from Vancouver Island. Biol. Bull. 169: 638-651.

Palmer, A.R. 1990. Predator size, prey size, and the scaling of vulnerability: hatchling gastropods vs. barnacles. Ecology 71: 759-775.

Palmer, A.R., S.D. Gayron, & D.S. Woodruff. 1990. Reproductive, morphological, and genetic evidence for two cryptic species of Northeastern Pacific *Nucella*. Veliger. 33: 325-338.

Rittschof, D. & A.B. Brown. 1986. Modification of predatory snail chemotaxis by substances in bivalve prey odours. Malacologia. 27: 281-290.

Rowley, R.J. 1989. Settlement and recruitment of sea urchins (*Strongylocentrotus* spp.) in a sea-urchin barren ground and a kelp bed: are populations regulated by settlement or post-settlement processes? Mar. Biol. 100: 485-494.

Rumrill, S.S. 1990. Natural mortality of marine invertebrate larvae. Ophelia. 32: 163-198.

Sarver, D.J. 1979. Recruitment and juvenile survival in the sea hare *Aplysia juliana* (Gastropoda: Opisthobranchia). Mar. Biol. 54: 353-361.

Smith, K.N. & W.F. Herrnkind. 1992. Predation on early juvenile spiny lobsters *Panulirus argus* (Latreille): influence of size and shelter. J. Exp. Mar. Biol. Ecol. 157: 3-18.

Spight, T.M. 1975. On a snail's chances of becoming a year old. Oikos. 26: 9-14.

Spight, T.M. 1982. Population sizes of two marine snails with a changing food supply. J. Exp. Mar. Biol. Ecol. 57: 195-217.

Strathmann, R.R. 1975. Toward understanding complex life cycles of benthic invertebrates. In: The Ecology of Fouling Communities. Ed. J.D. Costlow. Duke University Marine Laboratory, Beaufort, NC. pp. 1-20.

Strathmann, R.R. 1985. Feeding and non-feeding larval development and life-history evolution in marine invertebrates. Ann Rev. Ecol. Syst. 16: 339-361.

Thorson, G. 1966. Some factors influencing the recruitment and establishment of marine benthic communities. Neth. J. Sea Res. 3: 267-293.

Underwood, A.J. 1979. The ecology of intertidal gastropods. Adv. Mar. Biol. 16:111-210.

Underwood, A.J. and P.G. Fairweather. 1989. Supply-side ecology and benthic marine assemblages. Trends Ecol. Evol. 4: 16-20.

Vadas, R.L., W.A. Wright, and S.L. Miller. 1990. Recruitment of *Ascophyllum nodosum*: wave action as a source of mortality. Mar. Ecol. Prog. Ser. 61: 263-272.

Wahle, R.A. 1992. Body-size dependent anti-predator mechanisms of the American lobster. Oikos. 65: 52-60.

Wahle, R.A. & R.S. Steneck. 1992. Habitat restrictions in early benthic life: experiments on habitat selection and in situ predation with the American lobster. J. Exp. Mar. Biol. Ecol. 157:91-114

Williams, L.G., Rittschof, D., B. Brown, & M.R. Carriker. 1983. Chemotaxis of oyster drills *Urosalpinx cinerea* to competing prey odours. Biol. Bull. 164: 536-548.

CHAPTER II

Feeding habits of newly hatched juveniles of an intertidal predatory gastropod, *Nucella emarginata*.[1]

Introduction

The feeding habits of adult gastropods have been extensively studied (see reviews by Hughes, 1980, 1986, and by Crothers, 1985), particularly those of thaidine gastropods (Connell, 1970; Hughes and Dunkin, 1984; Palmer, 1984; Brown and Richardson, 1987; Gosselin and Bourget, 1989). Thaidine gastropods feed mainly on mussels and barnacles (Palmer, 1984, 1988; Crothers, 1985). Few studies, however, have examined the feeding habits of very young thaids. Largen (1967) reported that young *Nucella lapillus* feed on three species of barnacles and at least six species of molluscs, including conspecifics. Young *N. emarginata* are known to attack the barnacles *Balanus glandula* Darwin and *Chthamalus dalli* Pilsbry (Palmer, 1990). Juvenile snails in both these studies, however, were at least a few weeks old at the time feeding was confirmed and prey were identified. The feeding habits of thaids during the first days after emerging from their egg capsule have not been examined and no attempts to detect ontogenetic shifts in the mode of feeding have been reported. However, ontogenetic shifts in food use are common among aquatic invertebrates (Neill and Peacock, 1980; Davies et al., 1981; Town, 1981; Werner and Gilliam, 1984; Reid et al., 1990). Few documented cases exist for predatory gastropods, but substantial shifts, where early juveniles and adults depend on different food resources, have been reported. Bernard (1967) found that *Polinices lewisi*, a naticid snail that feeds on clams as an adult, is a herbivore during the first five to six months of its life. *Retusa obtusa*, an opisthobranch, feeds on radiolarians during the first five to six months, after which it gradually changes to a diet of the snail, *Hydrobia ulvae* (Berry,

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[1] A version of this chapter has been published.
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1989). In addition, changes in diet (*Nucella lapillus*, Hughes et al., 1992) and in drill site (*N. emarginata*, Hart and Palmer, 1987) have been reported for late juvenile thaids.

In this study, I examine *Nucella emarginata* (=*Thais emarginata*) (northern) (cf. Palmer et al., 1990), an intertidal predatory gastropod, to determine: 1) if newly hatched individuals initiate predatory feeding immediately after emerging from their egg capsule, and if not, 2) if newly hatched *N. emarginata* employ non-predatory (alternate) modes of feeding. Also, I determine: 3) which species hatchlings will consume once they have started attacking prey, and 4) if the feeding habits of hatchlings persist through to adulthood. The onset of predatory feeding by this organism can readily be detected because it attacks prey by drilling through their shell, and even brief, incomplete attacks can be recognized (Palmer, 1990; Gosselin, pers. obs.). The term "hatchling" is used here to describe juvenile *N. emarginata* from the moment they emerge from their egg capsule until they reach a shell length of 3 mm.

Materials and methods

1. Study site and organism

The present study was carried out in Barkley Sound, British Columbia, Canada. *Nucella emarginata* adults (15 - 22 mm shell length) and ripe egg capsules (unplugged capsules containing fully developed individuals that have not yet emerged) were collected at Kirby Point (48°50'85"N, 125°12'40"W), a site exposed to intense wave action; prey were collected at Kirby Point and at Dixon Island (48°51'15"N, 125°06'90"W). Experiments were conducted at the Bamfield Marine Station between June 1990 and July 1992.

Nucella emarginata embryos develop within benthic egg capsules. Consumption of nurse eggs is completed before the late veliger stage is reached, and final development is at the expense of their reserves (Leboeuf, 1971). Even when few veligers are present within a capsule, consumption of nurse eggs ceases well before hatching, and excess nurse eggs remain unused (T. Rawlings, pers. com.). Individuals emerge as crawl-away juveniles. Sizes of newly hatched *N. emarginata* range from 0.9 to 1.8 mm, measured from the apex to the tip of the siphonal canal (Spight, 1976; Gosselin, pers. obs.). For the experiments described herein, I used hatchlings that had been spawned in the field and had undergone complete larval development in their natural environment. Ripe capsules were collected from the field and placed in cages in flowing seawater in the laboratory. Only hatchlings emerging within 24 hours were used in the following experiments, thus ensuring that all hatchlings were of identical age (time of emergence is considered t=0). Hatchlings had no access to potential food items prior to their use in these experiments.

Three cage sizes were used: 1) "large": modified food containers, 95 x 95 x 60 mm; 2) "medium": modified plastic vials, 39 mm diam. x 62 mm long; and 3) "small": modified centrifuge micro test tubes, 11 mm diam. x 14 mm long. All cages were made by cutting out sections of the walls and covering these openings with 610 µm mesh screen.

2. Age at first attack

Two experiments were conducted to determine the age at which *Nucella emarginata* first attacks prey. In these experiments, single hatchlings were placed with three small *Mytilus* spp. (1 - 4 mm shell length) in small cages in flowing seawater. These cages ensured that hatchlings and mussels were in close proximity at all times. After regular time intervals, cages were recovered and each mussel was examined under a dissecting microscope for evidence of predation. A new set of 25 cages was examined for each observation time. Even a slight abrasion of a mussel's shell, by a hatchling that was starting to drill, could be recognized, allowing positive identification of all complete and incomplete attacks. As each cage contained only one hatchling, the proportion of hatchlings attacking prey could be calculated for each period. The first experiment was carried out in March 1992 with newly hatched individuals (<18 hour old); cages were recovered after 5, 10, 15, and 20 days. In the second experiment, carried out in June 1992, cages containing newly hatched individuals were recovered after 1, 3, 5, 7, 10, and 15 days. To verify that the results reflected an actual ontogenetic pattern, unfed 10-day old hatchlings were placed in the same conditions for 1, 3, and 5 days. Both sets of hatchlings for the June experiment (<18 hour and 10-day old) were obtained from the same sample of egg capsules.

3. Effects of experimental conditions on the onset of predatory feeding

To determine if the experimental conditions affected the onset of predatory feeding, I modified conditions that appeared most likely to influence foraging behaviour. Specifically, 1) cage size (medium; large); 2) prey type (*Balanus glandula*; *Chthamalus dalli*; *Mytilus* spp.); 3) cage contents (empty; tufts of *Cladophora columbiana* Collins *in* Setchell *et* Gardner); and 4) location (laboratory tanks; field). Medium cages each received 10 hatchlings (<24-hours old), large cages received 15 hatchlings. *B. glandula*, *C. dalli*, and *Mytilus* were used since they were found to be attacked by juvenile snails in our preliminary trials. *Cladophora* is an intertidal filamentous algae in which hatchlings are frequently found (chapter IV). The "field" cages were strapped to boards set in the intertidal zone at Dixon Island. After five days all cages were opened and each potential prey item was examined under a dissecting microscope for evidence of attacks by hatchlings. In addition, prey density within each cage was calculated to determine if this factor influenced the outcome of these trials. Prey densities were expressed as numbers of individuals per unit internal surface area of the cage.

4. Non-predatory modes of feeding

Use of food types other than live animals (alternate food types) by *Nucella emarginata* hatchlings was examined indirectly by determining growth, survival, and organic content of hatchlings raised with alternate food types.

4.1 Growth and survival

To determine whether hatchlings rely on alternate food types, I compared growth rates and survival of newly hatched individuals raised in five different food type treatments described below. Newly hatched *N. emarginata* were individually marked by applying colour codes to their shell (for method, see appendix 1). This allowed me to exclude from analysis the data from hatchlings that died during the experiment or were accidentally killed during manipulations. Initially, each hatchling was measured (shell length) and placed in one of the five following treatments:

1) All food: barnacles (*B. glandula* and *C. dalli*), mussels (*Mytilus* spp.), and *Lasaea* spp.. Unfiltered seawater.

2) No food: no food item. Filtered seawater.

3) Mussel feces: feces from *Mytilus edulis* L. and *Mytilus californianus* Conrad were added every 10 days for the first 30 days. Unfiltered seawater.

4) *Cladophora*: approximately 1 cm^3 of *Cladophora columbiana* was added to the cages. Biofilm was also provided in this treatment by including one rock (unsterilized) collected from the intertidal. Rocks and *Cladophora* tufts were examined initially under a dissecting microscope to ensure no other food items were present. Filtered seawater.

5) Barnacle moults: moults of *B. glandula* and *C. dalli* were provided every 10 days for the first 30 days. Filtered seawater.

Filtered seawater was obtained by passing water through a 1 μm filter. Each food type treatment was replicated in three large cages, with seven hatchlings per cage. Cages were separately placed in aerated 10 litre containers without continuous water flow. To prevent hatchlings in the no food, mussel feces, and barnacle moult treatments from having access to diatoms or bacterial growth, seawater was UV sterilized. The other treatments also received sterilized seawater to standardize experimental conditions. Seawater was changed approximately every 30 days. Sterilized rocks, boiled for 10 minutes, were added to all cages to provide a natural substrate. Hatchlings were measured and inspected for mortality after 30 and 50 days. Subsequently they were periodically examined for mortality until the conclusion of the experiment after 190 days.

4.2 Organic content

If hatchlings feed on alternate food sources, their total organic content should be sustained or increased. To examine this, one-day old unmarked hatchlings (size range 1.18 to 1.37 mm shell length) were placed in four food type treatments: 1) no food; 2) mussel feces; 3) *Cladophora*; and 4) barnacle moults. These experimental conditions were prepared as in the above growth and survival experiment. On day 1, the organic carbon content of 51 hatchlings (three per test tube = 17 replicates) was measured by dichromate oxidation against a glucose standard, using the method described by McEdward and Carson (1987). Organic carbon weight (μg) of hatchlings, including shells, was then converted to organic matter (OM) by the formula: 1 μg C = 2.5 μg OM (McEdward and Carson, 1987). Organic carbon weight can also be converted to joules to determine the total energy content (McEdward and Carson, 1987). The above method was also used to determine the total organic content of hatchlings after 20 days in each treatment.

5. Identification of hatchling prey

To identify the species of live animals that *Nucella emarginata* hatchlings consume, 10 species of intertidal invertebrates were separately offered to 15 day-old unfed hatchlings: three cirripedes (*B. glandula*, *C. dalli*, *Pollicipes polymerus* (=*Mitella polymerus*) Sowerby), four bivalves (*Mytilus* spp., *Lasaea* spp., *Hiatella arctica* (L.), *Musculus taylori* (Dall)), two limpets (*Lottia digitalis* (Rathke), *Lottia pelta* (Rathke)), and a snail (*Littorina scutulata* Gould). These species were common in the field at shore levels where *N. emarginata* is found (Gosselin, pers. obs.). The barnacle *Semibalanus cariosus* (Pallas) was not offered in the trials due to the scarcity of small individuals when hatchlings were available. Each potential prey species was separately offered to single hatchlings in small cages, 15 replicate cages per species. An additional set of 15 cages, each containing four hatchlings, tested for cannibalism. After five days in flowing seawater the contents of the cages were examined for evidence of predation.

6. Use of hatchling prey by adults

Species successfully attacked by hatchlings were offered to adult *Nucella emarginata* to determine if adults would consume the same species. These prey species were separately offered to single adults in medium cages, 15 replicate cages per prey species. After five days, the contents were inspected for evidence of predation.

Results

1. Age at first attack

Most *N. emarginata* would not attack small *Mytilus* spp. during the first three days after emerging from their egg capsule (Fig. II-1). The proportion of individuals attacking *Mytilus* then increased with time: after 10 days, at least 80 % had attacked. When unfed 10-day old hatchlings were placed in the same conditions, however, the proportion of individuals that had attacked prey after one day was twice that of newly hatched individuals after one day (Fig. II-1). The proportion of 10-day hatchlings that had attacked after three days with *Mytilus* (84%) was similar to that of <18 hour hatchlings enclosed for 10 to 15 days with *Mytilus*. There was no significant difference between the sizes of attacking and non-attacking <18 hour hatchlings after one day (ANOVA: F=2.71, p=0.11, n=25) or after three days with prey (F=0.49, p=0.49, n=25).

2. Effects of experimental conditions on the onset of predatory feeding

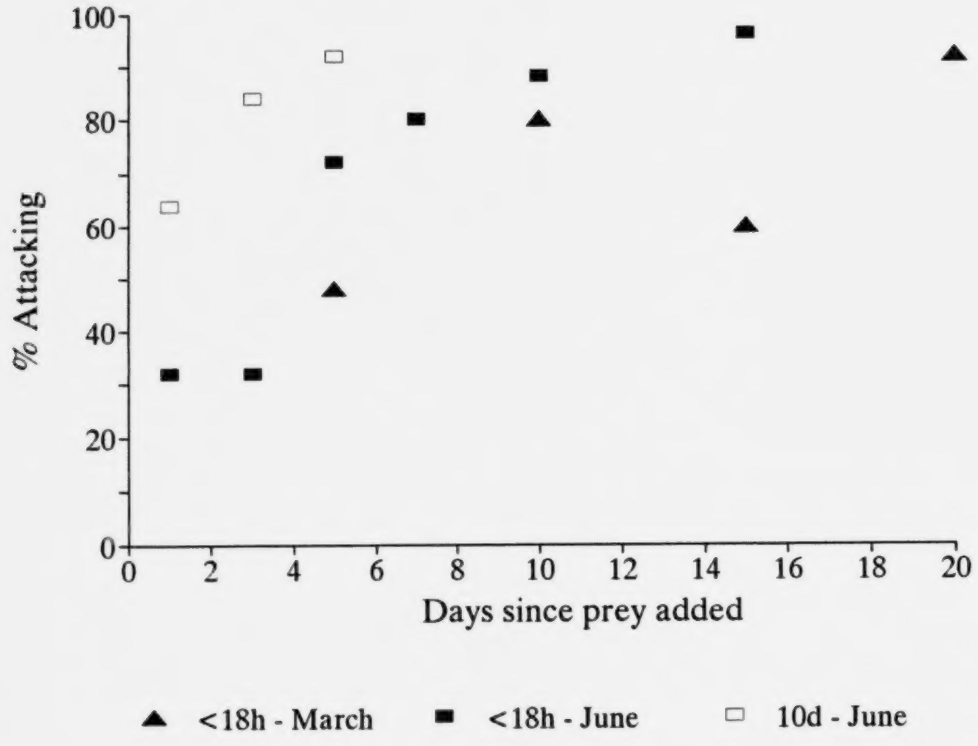
The highest attack rates (# attacks per hatchling) were obtained in cages containing small mussels (Table II-1). Even then, however, at least 57 % of the hatchlings did not attack prey, although several were found crawling over prey items. In addition, since certain hatchlings will attack two or three times over a five day period (chapter V), the proportion of hatchlings that actually attacked prey was probably smaller than the attack per hatchling values. Also, the regression between attack rate and prey density was not significant (F=1.73, p=0.20, n=32; pooled data from all experimental conditions and from the "age at first attack" experiment). Regardless of prey density, prey type, cage size, location of cages, or inclusion of *Cladophora*, most hatchlings did not attack prey during the five day period.

3. Non-predatory modes of feeding

3.1 Growth and survival

Growth of hatchlings in the alternate food type treatments (mussel feces, *Cladophora*, barnacle moults) were not significantly different from hatchlings in the no

Figure II-1. Percentage of *Nucella emarginata* hatchlings attacking small *Mytilus* spp.. Hatchlings were individually placed in small cages with three small *Mytilus*. Two sets of hatchlings were placed with prey within 18 hours of emerging from their egg capsules, in March and June 1992. A third set of unfed hatchlings were placed in small cages with *Mytilus* 10 days after emergence. Each value was calculated from a separate set of 25 replicates.



% Attacking
100
80
60
40
20
0
0
2
4
6
8
10
12
14
16
18
20
Days since prey added
▲ <18h - March
■ <18h - June
□ 10d - June

TABLE II-1

Number of attacks by *Nucella emarginata* hatchlings, when placed in 10 different sets of experimental conditions, during the first five days after emerging from their egg capsules. *B. glandula* and *C. dalli* shell diameters measured along rostro-carinal axis. Cage sizes: Large = 95 x 95 x 60 mm (15 hatchlings / cage), Medium = 39 mm diam. x 62 mm long (10 hatchlings / cage). "Field" cages were secured in the intertidal zone for the five day period. A small quantity of *Cladophora columbiana*, a filamentous algae, was added to certain cages to provide a typical microhabitat. Each experimental condition was replicated in three cages.

Prey Species	CONDITIONS			Attacks per hatchling[1] $\bar{x} \pm$ SD
	Cage	Location	Additional contents	
Balanus glandula (1.2-12.6 mm shell diameter)	Large	Lab.		0.07 ± 0.12
	Large	Field		0.09 ± 0.04
	Medium	Lab.		0.20 ± 0.26
Chthamalus dalli (1.1-5.7 mm shell diameter)	Large	Lab.		0.07 ± 0.07
	Large	Field		0.13 ± 0.12
	Medium	Lab.	*Cladophora*	0.13 ± 0.15
Mytilus spp. (1.0-5.0 mm shell length)	Large	Field		0.13 ± 0.13
	Large	Lab.		0.43 ± 0.32
	Medium	Lab.	*Cladophora*	0.43 ± 0.40
	Medium	Lab.		0.27 ± 0.12

[1] Total attacks per cage, including incomplete attacks, was divided by the number of hatchlings per cage to determine the number of attacks per hatchling.

food treatment during the two consecutive periods (Table II-2). Hatchlings in the no food and alternate food type treatments increased in length by an average of 6.15 % of initial length during the first 30 days, while hatchlings in the all food treatment grew by an average of 66.4 %. Predatory feeding is therefore necessary for substantial growth to occur. In addition, hatchlings in the alternate food type treatments did not survive longer than those in the no food treatment (Fig. II-2).

3.2 Organic content

The organic content of hatchlings after 20 days in the three alternate food type treatments were not significantly different from that of hatchlings in the no food treatment (Table II-3). Yet, the organic content of hatchlings in the no food treatment on day 21 was significantly lower than on day 1 (Table II-3), indicating that the 20 day period was sufficient for the organic content to decrease by a measurable quantity.

4. Identification of hatchling prey

Six species of intertidal invertebrates were attacked by *Nucella emarginata* hatchlings (Table II-4); at least three successful attacks were recorded on each of these species. All hatchlings in the *Mytilus* replicates were successful in drilling through the mussel's shell. Only one attack on *Hiatella arctica* was recorded: the borehole was superficial and the shell was not successfully drilled through. Conspecifics were not attacked.

5. Use of hatchling prey by adults

Adult *N. emarginata* did not attack three of the six species that were consumed by hatchlings (Table II-5). While *P. polymerus* was not attacked by adults in the feeding trials, adults have been observed feeding on them in the field, although infrequently (Gosselin, pers. obs.).

TABLE II-2

Initial sizes (age < 24 hours) and growth (shell length increment) of *Nucella emarginata* hatchlings when offered alternate food types. Sample sizes given in parentheses. As a result of mortality, the number of hatchlings per treatment ranged from 12 to 18.

Food type treatment	Initial shell length (mm)[1] $\bar{x}$ ± SE	Growth Days 0-30 (mm) $\bar{x}$ ± SE	SNK[2]	Growth Days 30-50 (mm) $\bar{x}$ ± SE	SNK[2]
All food	1.31 ± 0.04 (18)	0.87 ± 0.10 (18)	A	1.07 ± 0.11 (17)	A
No food	1.42 ± 0.05 (17)	0.03 ± 0.02 (17)	B	0 ± 0 (16)	B
Mussel feces	1.36 ± 0.06 (15)	0.11 ± 0.03 (15)	B	0 ± 0 (14)	B
Cladophora	1.38 ± 0.05 (13)	0.10 ± 0.03 (13)	B	-0.003 ±0.006 (12)	B
Barnacle moults	1.31 ± 0.04 (18)	0.10 ± 0.02 (18)	B	0.009 ±0.004 (18)	B
ANOVA F	1.12	45.14		82.12	
p	0.35	<0.0001		<0.0001	

[1] Calculation of average initial hatchling sizes was based on the measurements of individuals still alive on day 30.

[2] Student-Neuman-Keuls grouping at $\alpha=0.05$: means with the same letter are not significantly different.

Figure II-2. Survival of *Nucella emarginata* hatchlings in five food type treatments. Twenty-one hatchlings were initially placed in each treatment. The % surviving hatchlings on day 120 in the mussel feces, *Cladophora*, and barnacle moult treatments were not significantly different from that in the no food treatment (G-test, α=0.05; G value adjusted using Williams' correction; Sokal and Rohlf, 1981).

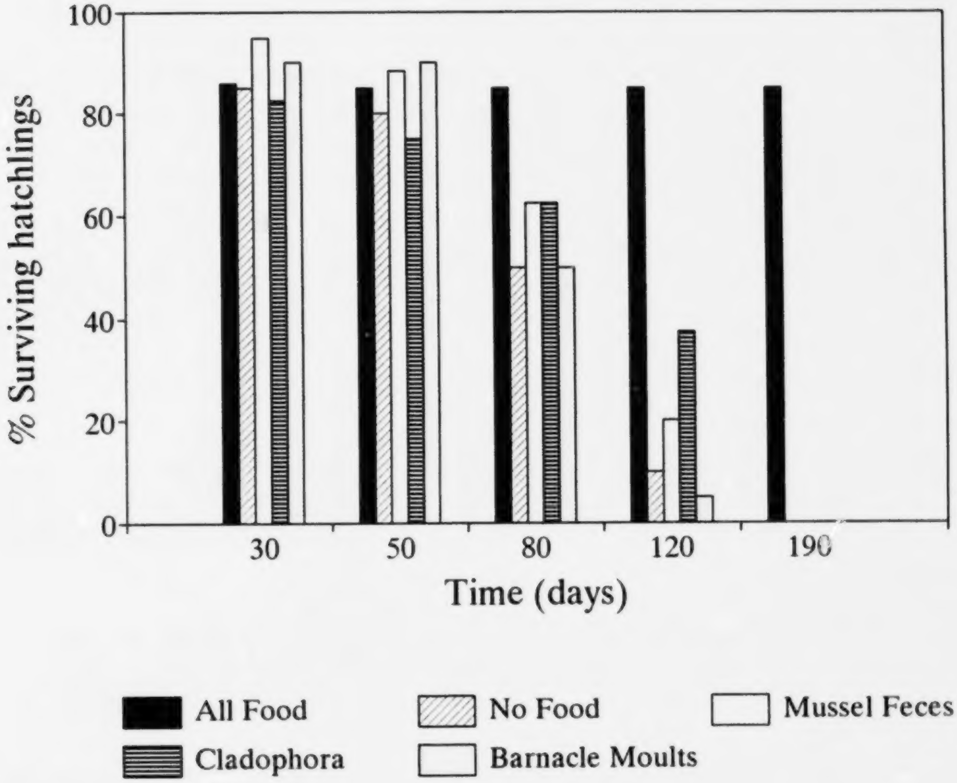

100
80
60
40
20
0
% Surviving hatchlings
30
50
80
120
190
Time (days)
All Food
No Food
Mussel Feces
Cladophora
Barnacle Moults

TABLE II-3

Total organic matter (OM) per *Nucella emarginata* after hatching (day 1) and after 20 days in four food type treatments.

	Total OM (μg)			ANOVA[1]	
	x̄	SE	n	F	p
Day 1	66.61	2.49	17		
Day 21:				6.52	0.017
No food	55.42	3.86	11	1.21	0.368
Mussel feces	58.84	5.38	9		
Cladophora	55.98	3.90	11		
Barnacle moults	63.41	6.00	9		

[1] ANOVAs were used to compare OM on day 1 with OM in no food treatment on day 21, and also to compare OM values among the four treatments on day 21.

TABLE II-4

Number of *Nucella emarginata* hatchlings (15 days old) attacking 11 species of intertidal invertebrates. For each species, 15 small cages each contained one hatchling and three individuals of the listed species for five days. The *N. emarginata* treatment consisted of four hatchlings per cage. Sizes of *P. polymerus*, *C. dalli*, and *B. glandula* are shell diameters, measured along the rostro-carinal axis. All other prey sizes are shell lengths.

Species	Size range (mm)		# of attacking hatchlings
	min.	max.	
Pollicipes polymerus	1.1	2.7	8
Chthamalus dalli	1.9	4.9	12
Balanus glandula	2.8	5.6	12
Mytilus spp.	1.7	4.3	15
Musculus taylori	1.0	3.5	8
Lasaea spp.	1.3	3.0	7
Hiatella arctica	3.0	6.8	1
Lottia pelta	1.8	3.6	0
Lottia digitalis	2.1	3.9	0
Littorina scutulata	1.3	5.0	0
Nucella emarginata	1.0	1.7	0

TABLE II-5

Number of *Nucella emarginata* adults (15 - 22 mm shell length) attacking the prey of hatchling snails. For each species, 15 medium cages each contained one adult and at least three individuals of the listed species for five days. Sizes of *P. polymerus*, *C. dalli*, and *B. glandula* are shell diameters, measured along the rostro-carinal axis. All other prey sizes are shell lengths.

Species	Size range (mm)		# of attacking snails
	min.	max.	
Pollicipes polymerus	8	21	0
Chthamalus dalli	2	5	10
Balanus glandula	2.5	11	15
Mytilus edulis	10	22	15
Musculus taylori	1.5	4.5	0
Lasaea spp.	2	3.5	0

Discussion

1. Onset of predatory feeding

Even when placed directly on prey items, most *Nucella emarginata* hatchlings younger than three days would not attack despite numerous changes to the experimental conditions. Instead, most began attacking prey 3 - 10 days after hatching. The high proportion of 10-day old hatchlings that attacked during the first three days of enclosure with prey suggest that the proportion of feeding individuals increases with age regardless of handling disturbance.

Premature emergence due to handling disturbance is not believed to be responsible for the low attack rates of newly hatched *N. emarginata*. The collection and handling of the capsules were not likely to produce disturbance in excess of what is normally experienced at Kirby Point, a site frequently subjected to severe wave impaction. Temperature shock was also unlikely, since surface water temperature differed from laboratory water temperature only by approximately 1 °C. Although the chemical composition of the water was not analyzed, the composition of field and laboratory seawater were not likely to differ significantly given that the station's seawater system had been in operation for several years, and that the seawater intake was located at a distance <200 m from the station, near the entrance of the Bamfield Inlet. A late onset of predatory feeding by newly hatched *N. emarginata* has been observed consistently in several preliminary feeding trials carried out between 1990 and 1992, with hatchlings from exposed and protected sites in Barkley Sound. Thus, it appears that the late onset of predatory feeding in *N. emarginata* is an actual ontogenetic pattern. Also, this feeding pattern is not likely to reduce hatchling survivorship, as most individuals can survive more than 50 days without prey (Fig. II-2).

The late onset of predatory feeding did not correspond to a period of transient use of mussel feces, *Cladophora*, biofilm (included in the *Cladophora* treatment), or barnacle moults. These alternate food types did not increase growth, survival time, or organic content relative to the hatchlings that had been starved. Consequently, no ontogenetic shift in mode of feeding was detected in *N. emarginata*.

2. Hatchling prey

Of the species that were offered, hatchlings only consumed bivalves (three species) and cirripedes (three species) (Table II-4). Drilled empty shells of small individuals of each of these six species have been found in the field when sampling microhabitats containing hatchlings (Gosselin, pers. obs.). Drill holes were of similar size and position as those produced by hatchlings in the laboratory, suggesting that hatchlings also feed on these organisms in the field.

Adult *N. emarginata* did not consume *M. taylori* and *Lasaea*. This may be due to the small size of these organisms, which have adult shell sizes no larger than 5 mm (Kozloff, 1987). Similarly, adults would not attack *Mytilus* spp. smaller than 5 mm. Yet, adults did consume many *C. dalli* measuring only 3 - 5 mm shell diameter. Therefore, *N. emarginata* may be unable to handle relatively small prey that are not firmly attached to a substratum. Although no ontogenetic shift in mode of feeding was observed in *N. emarginata*, at least two species consumed by hatchlings cease to be used during ontogeny.

3. Survival during prolonged periods of starvation

The ability of *N. emarginata* hatchlings to survive for extended periods without food is surprising. Hatchlings can feed on several species that are common intertidally, and are therefore likely to have good access to prey. Prey will be inaccessible, however, if embryos are unable to exit ripe egg capsules. This can occur if the young snail does not fit through the opening, if a capsule mate too large for the opening has blocked the exit, or if the opening is irregular (Gosselin, pers. obs.). In the field, capsular material will break down a few days to several weeks after the capsule has become unplugged (pers obs.). Given their ability to survive for extended periods without feeding, *N. emarginata* trapped within their egg capsule might survive until the walls deteriorate.

4. Conclusions

Predatory gastropods might be expected to start feeding immediately after hatching because rapidly attaining a larger size will reduce their vulnerability to predation, desiccation, and wave action (Faller-Fritsch, 1977; Underwood, 1979) to which very small individuals are highly vulnerable (Branch, 1975; Underwood, 1979; Werner and Gilliam, 1984). An immediate onset of feeding, however, might conflict with other requirements. Juveniles emerging from egg capsules are directly exposed to mortality factors until they reach protective microhabitats. If newly hatched snails stop to attack prey (e.g. by drilling through a prey's shell) before reaching a refuge, they extend the period of direct exposure to these mortality factors. I found that the shortest time required for 20-day old *N. emarginata* hatchlings to drill, consume, and discard a small mussel (1-2 mm shell length) was 22 hours (unpubl. data). Some had not yet discarded their prey after 48 hours. Thus, if newly hatched *N. emarginata* stop to attack prey before reaching a refuge, they remain exposed to mortality factors during at least two tidal cycles. The main requisite early in life may be to find protection while living off reserves remaining from the egg capsule (Feare, 1970). However, the onset of feeding does not appear to be triggered by external cues, such as finding a refuge; attack rates were not higher when hatchlings were placed in cages with *Cladophora*, in field cages, or in various other conditions (Table II-1). Alternatively, the late onset of feeding may serve to prevent or reduce cannibalism within the egg capsule (cannibalism by *Nucella lapillus* embryos was reported by Largen, 1967, and I have observed one case of predation within the egg capsule in *N. emarginata*). The late onset of predatory feeding could also be an indirect consequence of selective pressures to minimize encapsulation time, whereas hatchlings would emerge once fully mobile but before a complete development of the feeding apparatus (e.g. the radula). Additional information on the development, behaviour, and ecology of young juveniles is necessary to fully understand the causes and mechanisms producing the late onset of feeding in *N. emarginata*.

References

Bernard, F.R. 1967. Studies on the biology of the naticid clam drill *Polinices lewisi* (Gould) [Gastropoda Prosobranchiata]. Fish. Res. Bd. Can. Tech. Rep. No. 42. 41pp.

Berry, A.J. 1989. Factors implicated in the timing of breeding in two contrasted annual intertidal gastropods, *Retusa obtusa* (Montagu) and *Umbonium vestiarium* (L.). In: Reproduction, genetics and distributions of marine organisms. Proceedings of the 23rd European marine biology symposium. Eds. J.S. Ryland and P.A. Tyler, Olsen and Olsen, Fredensborg, Denmark. pp. 31-36.

Branch, G.M. 1975. Ecology of *Patella* species from the Cape Peninsula, South Africa. IV. Desiccation. Mar. Biol. 32: 179-188.

Brown, K.M. and T.D. Richardson. 1987. Foraging ecology of the southern oyster drill *Thais haemastoma* (Gray): constraints on prey choice. J. Exp. Mar. Biol. Ecol. 114: 123-141.

Connell, J.H. 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. Ecol. Monogr. 40: 49-78.

Crothers, J.H. 1985. Dogwhelks: an introduction to the biology of *Nucella lapillus* (L.). Field Studies. 6: 291-360.

Davies, R.W., F.J. Wrona, L. Linton, and J. Wilkialis. 1981. Inter- and intra-specific analyses of the food niches of two sympatric species of Erpobdellidae (Hirudinoidea) in Alberta, Canada. Oikos 37: 105-111.

Faller-Fritsch, R.J. 1977. Reproductive strategies of the winkle *Littorina rudis* in relation to population dynamics and size structure. In: Biology of Benthic Organisms. Proceedings of the 11th European Symposium on Marine Biology. Eds. B.F. Keegan, P.O. Ceidigh, and P.J.S. Boaden, Pergamon Press, Oxford, UK. pp. 225-231.

Feare, C.J. 1970. Aspects of the ecology of an exposed shore population of dogwhelks *Nucella lapillus* (L.). Oecologia 5: 1-18.

Gosselin, L.A. and E. Bourget. 1989. The performance of an intertidal predator *Thais lapillus*, in relation to structural heterogeneity. J. Anim. Ecol. 58: 287-303.

Hart, M.W. and A.R. Palmer. 1987. Stereotypy, ontogeny, and heritability of drill site selection in thaidid gastropods. J. Exp. Mar. Biol. Ecol. 197: 101-120.

Hughes, R.N. 1980. Optimal foraging theory in the marine context. Oceanogr. Mar. Biol. Ann. Rev. 18: 423-481.

Hughes, R.N. 1986. A Functional Biology of Marine Gastropods. John Hopkins University Press, Baltimore, USA. 245 pp.

Hughes, R.N., M.T. Burrows and S.E.B. Rogers. 1992. Ontogenetic changes in foraging behaviour of the dogwhelk *Nucella lapillus* (L.). J. Exp. Mar. Biol. Ecol. 155: 199-212.

Hughes, R.N. and S. de B. Dunkin. 1984. Behavioural components of prey selection by dogwhelks, *Nucella lapillus* (L.), feeding on mussels, *Mytilus edulis* L., in the laboratory. J. Exp. Mar. Biol. Ecol. 77: 45-68.

Kozloff, E.N. 1987. Marine Invertebrates of the Pacific Northwest. University of Washington Press, Seattle, WA. 511 pp.

Largen, M.J. 1967. The diet of the dog-whelk, *Nucella lapillus* (Gastropoda Prosobranchia). J. Zool. (Lond.) 151: 123-127.

Leboeuf, R. 1971. *Thais emarginata* (Deshayes): description of the veliger and egg capsule. Veliger. 14: 205-211.

McEdward, L.R. and S.F. Carson. 1987. Variation in egg organic content and its relationship with egg size in the starfish *Solaster stimpsoni*. Mar. Ecol. Prog. Ser. 37: 159-169.

Neill, W.E. and A. Peacock. 1980. Breaking the bottleneck: interactions of invertebrate predators and nutrients in oligotrophic lakes. In: Evolution and Ecology of Zooplankton Communities. Ed. W.C. Kerfoot, University Press of New England, Hanover, N.H. pp. 715-724.

Palmer, A.R. 1984. Prey selection by thaidid gastropods: some observational and experimental field tests of foraging models. Oecologia 62: 162-172.

Palmer, A.R. 1988. Feeding biology of *Ocenebra lurida* (Prosobranchia: Muricacea): Diet, predator-prey size relations, and attack behavior. Veliger. 31: 192-203.

Palmer, A.R. 1990. Predator size, prey size, and the scaling of vulnerability: hatchling gastropods vs. barnacles. Ecology. 71: 759-775.

Palmer, A.R., S.D. Gayron, and D.S. Woodruff. 1990. Reproductive, morphological, and genetic evidence for two cryptic species of Northeastern Pacific *Nucella*. Veliger. 33: 325-338.

Reid, R.G.B., R.F. McMahon, D. Ó Foighil, and R. Finnigan. 1992. Anterior inhalant currents and pedal feeding in bivalves. Veliger. 35: 93-104.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. W.H. Freeman and Co., New York, NY, Second edition. 859 pp.

Spight, T.M. 1976. Hatching size and the distribution of nurse eggs among prosobranch embryos. Biol. Bull. 150: 491-499.

Town, J.C. 1981. Prey characteristics and dietary composition in intertidal *Astrosole scabra* (Echinodermata: Asteroidea). N.Z. J. Mar. Freshwater Res. 15: 69-80.

Underwood, A.J. 1979. The ecology of intertidal gastropods. Adv. Mar. Biol. 16: 111-210.

Werner, E.E. and J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst. 15: 393-425.

CHAPTER III

Characterizing temperate rocky shores from the perspective of an early juvenile snail: the main threats to survival of newly hatched *Nucella emarginata.*

Introduction

In benthic marine organisms, the early juvenile period can be a time of considerable mortality (Thorson, 1966; Sarver, 1979; Jablonski and Lutz, 1983; Gosselin and Qian, submitted). In fact, mortality during this period can be as important as larval supply in determining recruitment (Osman et al., 1992). Substantial mortality of benthic early juveniles has been reported for macroalgae (Vadas et al., 1990; Brawley and Johnson, 1991; Benedetti-Cecchi and Cinelli, 1992), barnacles (Denley and Underwood, 1979; Young, 1991; Gosselin and Qian, submitted), bivalves (Bachelet, 1989), crabs (Orensanz and Galluci, 1988), limpets (Branch, 1975), nudibranchs (Sarver, 1979), and seastars (Keesing and Halford, 1992). Given that a considerable proportion of recruits may die during the early juvenile period, it may be during this period that particular traits and distribution patterns (e.g. colour, shell thickness, behavioural responses to predators, or the distribution of sessile organisms among microhabitats) are established that will characterize populations or local groups of organisms (Gosselin and Qian, submitted). Consequently, the main threats to the survival of early juveniles must be identified to understand the significance of larval and juvenile traits, to define the processes controlling recruitment, and to elucidate the significance of early life history strategies.

The term *vulnerability* is used here to refer to the likelihood that an organism will die when directly exposed to a given factor or to a specified set of conditions. An organism may be highly vulnerable to a particular factor, however, and yet rarely be killed by it in the field, for example as a result of preferences for microhabitats sheltering it from the influence of the factor. A vulnerability value therefore does not represent the likelihood of the organism being killed in the field. Rather, it indicates how important it is for the organism to avoid exposure to the factor: if an organism is highly vulnerable to a naturally occurring factor, it will almost certainly be killed unless it can avoid direct exposure to this factor. Hence, vulnerability measurements should be good indicators of the relative importance of individual factors as selective agents.

Intertidal habitats regularly cycle through periods of marine and quasi-terrestrial conditions, exposing their inhabitants to a variety of biotic and abiotic dangers. Accordingly, many factors have been reported to cause mortality of intertidal organisms (Table III-1). Although any of these factors may be locally important, predation and desiccation are the most widespread and best documented mortality factors (e.g. see Underwood, 1979). Because vulnerability to predators often decreases with increasing size (Paine, 1976; Vermeij, 1978, 1993), overall predation risk is highest when individuals are smallest and vulnerable to a broad range of sizes and species of predators (Thorson, 1966; Werner and Gilliam, 1984). Intertidal organisms are also expected to be most vulnerable to physical factors when they are very small, owing to their high surface to volume ratio (Foster, 1971; Vermeij, 1972; Wolcott, 1973). Few studies have examined the threats to survival of early juveniles in the intertidal zone. In addition, most existing reports only involve sessile organisms, and this information may be of limited relevance to motile organisms.

Early juveniles of many benthic invertebrates are difficult to study due to their small size, sensitivity, sparse distribution, and seasonal availability. Intertidal gastropods, however, are amenable to the study of early juvenile vulnerability because individuals can easily be relocated for laboratory and field experimentation, are relatively undisturbed by gentle handling (appendix 1), and are often abundant and accessible. Consequently, this study aims to characterize temperate rocky shores from the perspective of an early juvenile gastropod by identifying mortality factors that are most likely to impose substantial selective pressures during the early juvenile period. Specifically, I examine the vulnerability of newly hatched *Nucella emarginata* (Deshayes) (northern) (cf. Palmer et al., 1990), an intertidal prosobranch gastropod abundant along the rocky shores of northwestern North America, to high temperatures, desiccation, and predation (including the effects of grazers). The prevalence of these factors in the field is also assessed to estimate the importance of these factors for early juvenile survival.

TABLE III-1

Factors causing mortality of intertidal invertebrates on temperate rocky shores.

Factor	Organism(s)	Early juveniles?	Selected sources
Abiotic factors			
Desiccation	Barnacles	Y	Foster, 1971
	Limpets	N	Wolcott, 1973
	Limpets	Y	Branch, 1975
Dislodgement by waves	Mussels	N	Dayton, 1971
	Snails	Y	Faller-Fritsch & Emson, 1985
Freezing	Bivalves, gastropods, polychaetes	N	Blegvad, 1929
	Mussels	N	Paine, 1974
High temperature	Limpets	N	Branch, 1975
Ice scouring	Barnacles	N	Wethey, 1985
	Barnacles	N	Bergeron & Bourget, 1986
Impacts by water-borne debris	Barnacles	Y	Connell, 1961
	Mussels and other sessile organisms	N	Dayton, 1971
Reduced salinity	Snails	Y	Berry & Hunt, 1980
Biotic factors			
Dislodgement of hummocks	Barnacles on barnacles	N	Barnes & Powell, 1950

Dislodgement or ingestion by grazers ("bulldozing")	Snails on barnacles	Y	Petraitis, 1983
	Limpets on barnacles	Y	Miller & Carefoot, 1989
	Limpets on limpets	Y	Fletcher & Underwood, 1987
Immobilization by byssal threads	Mussels on snails	N	Petraitis, 1987
	Mussels on snails	N	Day, Barkai, & Wickens, 1991
Overgrowth, crushing or undercutting by competitors	Barnacles on barnacles	N	Connell, 1961
	Algae on barnacles	N	Bertness, 1989
	Algae on mussels	N	Dittman & Robles, 1991
Predation	Snails on barnacles	N	Connell, 1970
	Seastars on mussels	N	Paine, 1976
	Fish and conspecifics on juvenile crabs	N	Fernandez, Iribarne, & Armstrong, 1993 (also see review by Underwood, 1979)
Toxic algal blooms	Snails, fish, and crabs	N	Robertson, 1991

Materials and Methods

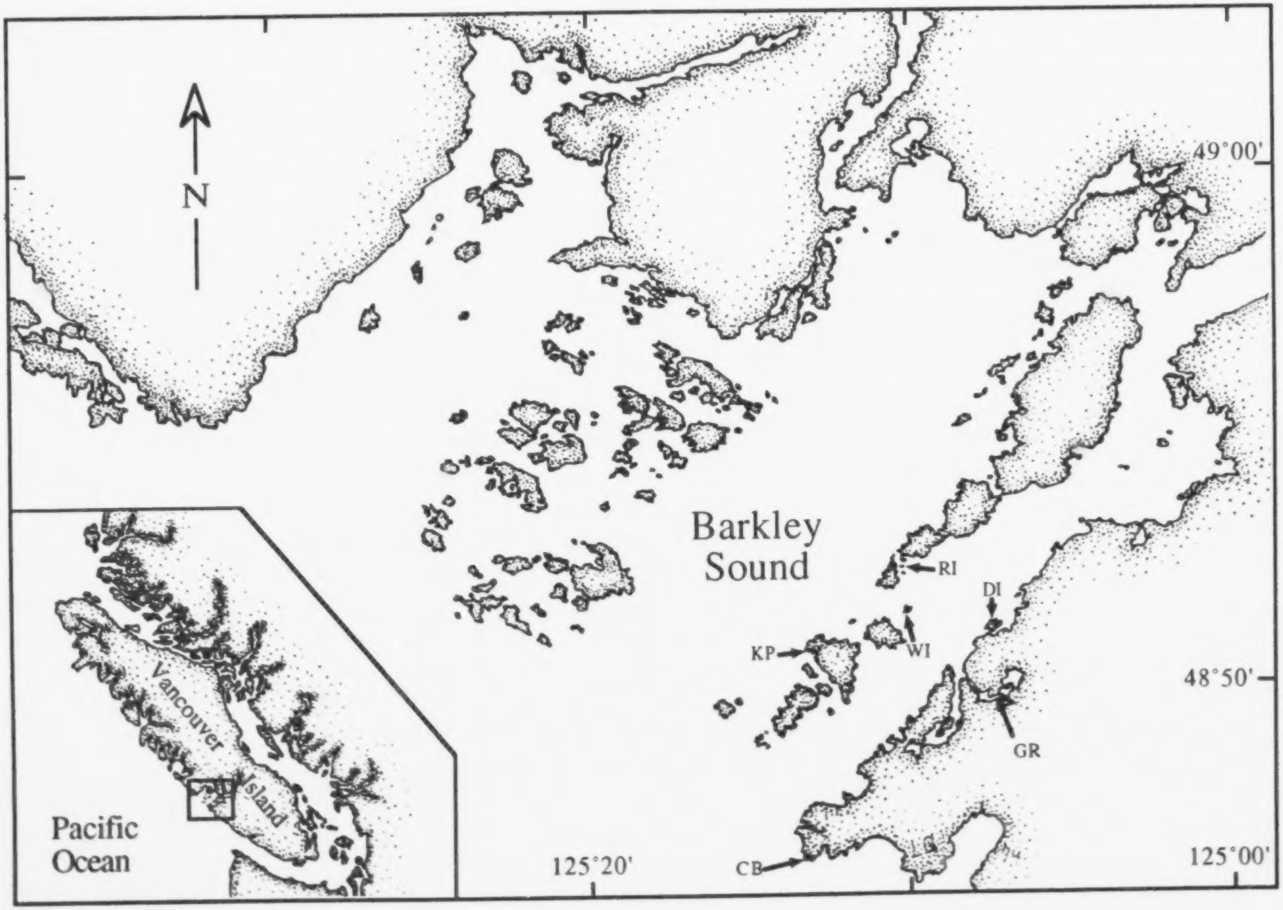
1. Study site and organism

This study was conducted at the Bamfield Marine Station and at nearby field sites in Barkley Sound, Vancouver Island, Canada (Fig. III-1), from May 1992 to September 1993. Ripe egg capsules (unplugged capsules containing metamorphosed individuals that have not yet emerged) were collected at Ross Islets (48°52'35" N, 125°09'65" W), Dixon Island (48°51'15"N, 125°06'90"W) and Kirby Point (48°50'85"N, 125°12'40"W). Hatchlings (0.9-1.8 mm shell length) that emerged in the laboratory during the first 48 hours after collecting the capsules were placed in a separate cage until later use; the age of the hatchlings used in each experiment could therefore be determined with an accuracy of 48 hours (time of emergence is considered t=0). Adult *Nucella emarginata* (16 - 26 mm shell length) were collected at Ross Islets (Fig. III-1). Snails were not used more than once in this study. In Barkley Sound, emersion of substrata at tidal heights colonized by *N. emarginata* will last six to nine hours, depending on tidal amplitude, tidal height, and surface water conditions (waves).

2. Maximum air and seawater temperatures in the field

Since most *Nucella emarginata* in Barkley Sound hatch during the summer (appendix 2), early juveniles may be exposed to high summer temperatures but very few will experience low winter temperatures. Maximum monthly air temperatures for the years 1986 to 1993 (P. Janitis, unpubl. data) were obtained from daily afternoon measurements ≈40 m from the shoreline on a property protected from the wind in Grappler Inlet (Fig. III-1). Maximum monthly summer seawater temperatures for 1986 to 1992 (N. Brand, unpubl. data) were also obtained from daily measurements (1 m depth) at Cape Beale lighthouse (48°47'20" N, 125°12'95" W), located on the open coast at the southern point of the entrance to Barkley Sound (Fig. III-1). Additional maximum seawater temperatures from within Barkley Sound were obtained for June to September of 1991 to 1993 from monthly measurements (10 - 30 cm depth) at Ross Islets, located 10.4 km from Cape Beale.

Figure III-1. Map of Barkley Sound showing study sites. CB = Cape Beale, DI = Dixon Island, GR = Grappler Inlet, KP = Kirby Point, RI = Ross Islets, WI = Wizard Islet.


N
49°00'
48°50'
125°20'
125°00'
Barkley Sound
RI
DI
WI
KP
GR
CB
Vancouver Island
Pacific Ocean

3. Vulnerability to high temperatures

Hatchling vulnerability to high temperatures was examined in controlled laboratory conditions in May 1993. To determine if hatchlings and adults are similarly vulnerable to high temperatures, adult snails were also included in the experiment, although in separate containers. Snails were exposed to temperatures selected as being slightly below (22 °C), close to (26 °C), or slightly higher than (30 °C) the highest they were likely to experience in the field (see below). Water temperature in the field and in the laboratory at the time of the experiment was ≈11 °C. For each temperature treatment, snails were placed within one of two sub-treatments: *emersion*: snails were placed in sealed 1.2 litre plastic containers lined with seawater-wetted cloth (5 mm layer) covered with 610 µm mesh screen to separate the snails from the cloth; *immersion*: caged snails (95 x 95 x 60 mm cages, with 610 µm mesh screen) were placed in 20 litre aquaria containing seawater. The emersion treatment provided constant maximum humidity conditions but allowed minimal contact with seawater, simulating field conditions in moist microhabitats, while the immersion treatment simulated conditions in small tidepools that warm up during low tide. These sub-treatments also ensured that the effect of temperature would be determined in the absence of desiccation stress. Eight-day old hatchlings and adults were exposed to the following conditions: 22 °C treatment: eight hours in an incubator at 22 °C; 26 °C treatment: one hour in an incubator at 16 °C, subsequently transferred to a second incubator at 21 °C for one hour, and then to a third incubator at 26 °C for eight hours; 30 °C treatment: one hour at 18 °C, one hour at 24 °C, and then eight hours at 30 °C. The intermediate temperatures at the start of the 26 °C and 30 °C treatments were included to roughly simulate the gradual rise in temperatures of intertidal substrata when the tide recedes. For the immersion sub-treatments, each incubator contained an aquarium with aerated seawater, and only the cages containing snails were transferred from one incubator to the next. At the end of the experiment, all snails were returned to tanks with flowing 11 °C seawater for 12 hours, after which each individual was examined under a dissection microscope. Snails not responding when their operculum was touched with a probe were recorded as dead. Hatchlings dying from heat or desiccation (next experiment) usually had darkened flesh and were easy to recognize.

4. Vulnerability to desiccation

4.1 Laboratory desiccation experiment

To determine if newly hatched *Nucella emarginata* can tolerate direct exposure to ambient air for the duration of a low tide, the survival of hatchlings after six to eight hours of emersion was assessed. Two-day old hatchlings were placed in an incubator on a shale rock plate (40 x 40 x 3 cm) wetted with seawater. For comparison, adult snails were also placed on a second similar plate in the same incubator. Since evaporation increases with increasing temperature, the experiment was repeated at 15, 22, and 25 °C to simulate a range of conditions likely to occur in the field; 22 °C is reached occasionally during the summer in the intertidal zone in Barkley Sound, while 25 °C occurs infrequently (see below). A fan in the incubator maintained a continuous, moderate flow of air throughout the experiment. In each treatment, a separate set of hatchlings and adults were recovered after one, two, four, and six hours; an additional set was also recovered after eight hours in the 22 °C treatment. Sample sizes for each observation interval were as follows: 15 °C: 5 hatchlings and 3 adults; 22 °C: 15 hatchlings and 10 adults; 25 °C: 20 hatchlings and 10 adults. Once removed from the incubator, snails were immediately placed in flowing seawater for 30 minutes; each individual was then examined for mortality. The period during which snails were left in flowing seawater before being examined for mortality in the high temperature and desiccation experiments ranged from 30 minutes to 24 hours. This is not believed to have affected the results, however, since live snails appeared to recover rapidly, emerging from their shell or even becoming active within 10 - 20 minutes in flowing seawater (pers. obs.). Approximate relative humidity was measured with a psychrometer at the start and end of the 22 °C and 25 °C treatments.

4.2 Field desiccation experiment

To determine the relevance of laboratory experiments to field conditions, *Nucella emarginata* hatchlings were also exposed to ambient conditions in the intertidal zone at Wizard Islet (48°51'45" N, 125°09'55" W) (Fig. III-1). Sunny, windy conditions coincided with an afternoon low tide on 11 September 1993, exposing intertidal organisms to high desiccation stress. Hatchlings were brought to the field and placed on three small shale rock plates (8 x 8 x 1 cm). These plates had remained in tanks with flowing seawater for two weeks prior to this experiment to allow the formation of a biofilm on the surfaces of the plates, as this might affect water retention and snail behaviour. Once in the field, the plates were put in a tray with seawater. Twenty hatchlings (8 - 10 days old) were placed on each plate. When all hatchlings had attached, the plates were gently removed from the water and placed on a mat (≈0.75 x 1 m) of filamentous algae, *Cladophora columbiana*, growing on an area of flat, horizontal rock. The contact between the plates and the seawater absorbed in the *Cladophora* mat helped maintain the plates at a temperature similar to the nearby substrata. Tidal height was approximately 1.8 m above Mean Lower Low Water (MLLW), a height at which *N. emarginata* snails and egg capsules are commonly found at that site. During the experiment, air temperature and relative humidity were measured 1 cm and 1 m above the plates using an Oakton model 37200-00 thermohygrometer. Based on the results of the laboratory experiments indicating high mortality during the first four hours, all hatchlings were recovered after four hours, returned to the laboratory, and placed in flowing seawater for 24 hours. Each individual was then examined for mortality.

5. Vulnerability to predation

Intertidal organisms most likely to kill newly hatched *Nucella emarginata* in the field were identified by offering hatchlings to individuals of 45 intertidal species. Potential predators were collected from Grappler inlet (wave-protected, 48°50'05" N, 125°06'90" W), Ross Islets (intermediate wave exposure), and Kirby Point (nearly fully exposed to ocean surge) (Fig. III-1). All of these locations supported substantial *N. emarginata* populations. An attempt was made to include most macroscopic intertidal grazers and predatory species that may co-occur with *N. emarginata* in the field. Grazers were included as potential predators because they can crush or ingest early juvenile barnacles (Connell, 1961; Miller and Carefoot, 1989), ascidians (Young and Chia, 1984), and limpets (Fletcher and Underwood, 1987) and thus may also be a threat to very small snails. Three to six individuals of each potential predator species were collected. Each individual was separately placed in a cage without food for two to three days prior to adding hatchlings. Ten 20-day old hatchlings were then added to each cage. The contents of each cage were examined after three days. Cage sizes were: large cages = 95 x 95 x 60 mm, and small cages = 39 mm diam. x 62 mm long, the latter being used for smaller potential predators.

6. Predator densities in the field

To determine the abundance of predators in the field, densities of the most common species that killed hatchlings in the laboratory (three hermit crabs and one shore crab) were assessed at three sites between 16 August and 7 September 1993, a time of year when hatchling and juvenile *Nucella emarginata* are generally abundant (appendix 2). Ross Islets, Wizard Islet, and Dixon Island sites (low-moderate, moderate, and moderate-high exposure to wave action, respectively) had previously been noted as supporting substantial densities of hermit crabs and shore crabs (pers. obs.). At each site, five quadrats (25 x 25 cm) were sampled at 1 m intervals along each of two 5 m transects running parallel to the shore at 1.2 to 1.8 m above MLLW (10 quadrats per site).

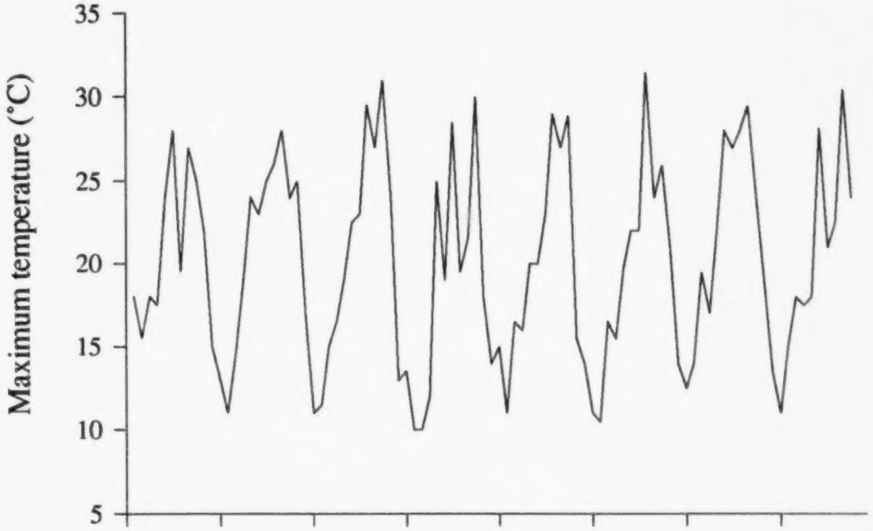
Results

1. Maximum air and seawater temperatures in the field

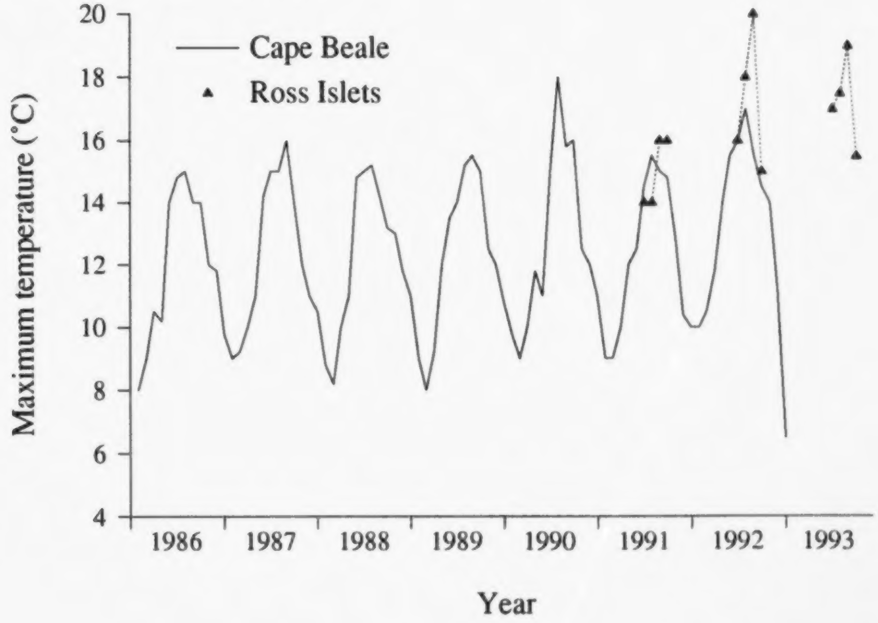
Air temperatures in Grappler Inlet remained below 30 °C in four of eight years (1986-1993, Fig. III-2a), and equalled or slightly exceeded 30 °C only on a few occasions in the other four years. The highest air temperature recorded over the eight year period was 31.5 °C (July 1991). Air temperatures in excess of 26 °C occurred only on a few days each summer, and these did not often coincide with afternoon low tides. Moreover, air temperatures in the intertidal zone in Barkley Sound on warm days were ≈4 - 8 °C cooler than at the site where temperatures were recorded in Grappler Inlet (pers. obs.). Thus, air temperature at low tide in the intertidal zone is unlikely to exceed 26 °C, and was not observed to exceed 24 °C during four summers of field work (1990-1993).

Figure III-2. Maximum monthly temperatures recorded in Barkley Sound from 1986 to 1993. a) maximum air temperatures in Grappler inlet; b) maximum surface seawater temperatures at Cape Beale (1 m depth) and Ross Islets (10 - 30 cm depth).

a) Air temperature



b) Seawater temperature



Seawater temperatures on the exposed coast did not exceed 18 °C between 1986 and 1992 (Cape Beale, Fig. III-2b). Surface waters became warmer within Barkley Sound than on the open coast during the summer, but did not exceed 20 °C over a three year period (Ross Islets, Fig. III-2b).

2. Vulnerability to high temperatures

Nucella emarginata hatchlings do not appear to be vulnerable to temperatures as high as 26 °C, as all hatchlings survived eight hours at 22 °C and 26 °C (Table III-2). Hatchling mortality did occur, however, at 30 °C. At this temperature, most hatchlings in the emersion sub-treatment died. Only one death was recorded among hatchlings immersed in 30 °C seawater. Hence, during low tide emersion, temperatures of ≈30 °C or higher could be lethal for hatchlings from Barkley Sound populations. Adults, however, survived well in all temperature treatments (Table III-2).

3. Vulnerability to desiccation

3.1 Laboratory desiccation experiment

No hatchling survived six hours of emersion at any of the three temperatures used in this study (Fig. III-3). Survival time decreased with increasing temperature. At 25 °C, all hatchlings were dead within two hours. Relative humidity within the incubator was: 22 °C treatment: initial = 86%, six hours = 80%, eight hours = 77%; and 25 °C treatment: initial = 84%, six hours = 66%. No humidity measurements were taken during the 15 °C treatment. Adult snails had 100% survival throughout all laboratory desiccation experiments.

3.2 Field desiccation experiment

All 20 hatchlings on each of the three plates set in the intertidal zone at Wizard Islet died during the four hours of direct exposure to low tide conditions. Relative humidity at 1 cm above the plates (Table III-3) was comparable to the measurements obtained in the laboratory experiments. These mortality results are in agreement with those obtained in the laboratory experiments, indicating that hatchling *Nucella emarginata*

TABLE III-2

Mortality of *Nucella emarginata* hatchlings and adults (16 - 25 mm shell length) after eight hours at different temperatures. Values represent average mortality rate (%) ± STD, each based on three replicates. Replicates consisted of eight hatchlings or four adults. Emersion sub-treatment: snails were placed in sealed containers maintaining constant maximum humidity. Immersion sub-treatment: snails were kept immersed in seawater.

	22 °C		26 °C		30 °C	
	Emersion	Immersion	Emers.	Immers.	Emers.	Immers.
Hatchlings	0±0	0±0	0±0	0±0	83.3±14.4	4.2±7.2
Adults	0±0	0±0	0±0	8.3±14.4	0±0	0±0

Figure III-3. Survival time of newly hatched *Nucella emarginata* when emersed for up to six hours (15 °C, 25 °C) or eight hours (22 °C). Hatchlings were placed in flowing seawater for 30 minutes before being examined for mortality. Each value represents the survival of a separate set of 5 (15 °C), 15 (22 °C) or 20 (25 °C) hatchlings.

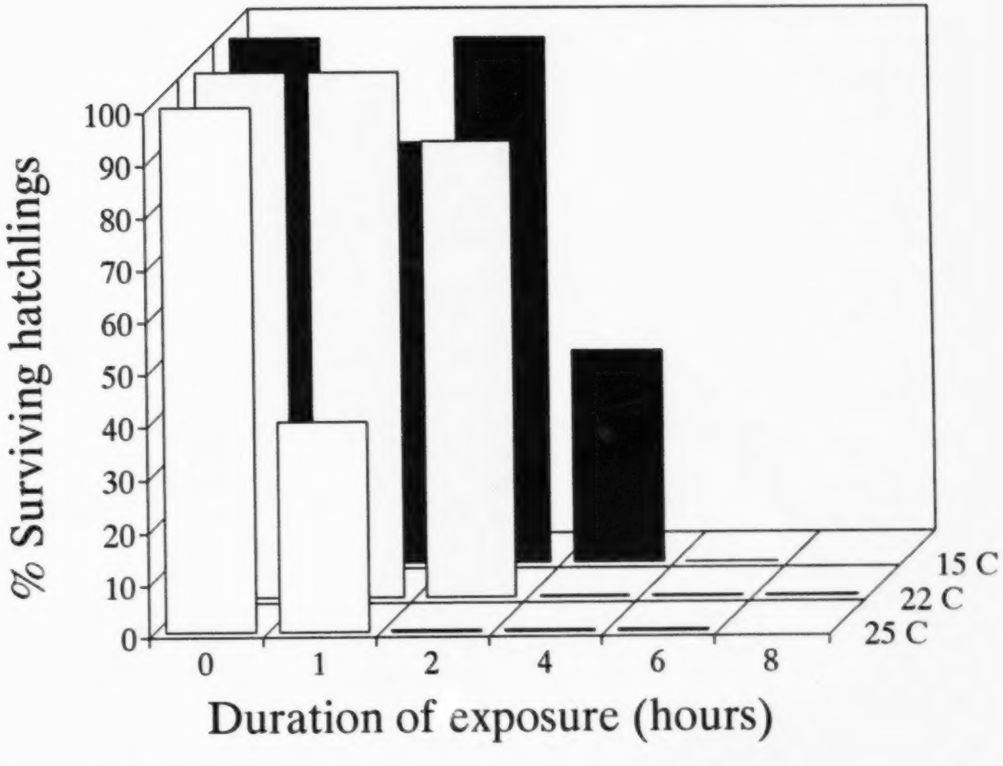

% Surviving hatchlings
100
90
80
70
60
50
40
30
20
10
0
0
1
2
4
6
8
Duration of exposure (hours)
15 C
22 C
25 C

TABLE III-3

Temperature and relative humidity measured above experimental rock plates at Wizard Islet on 11 September 1993. Measurements were carried out at low tide at ≈1.8 m above MLLW during the field desiccation experiment, which lasted from 14:00 h to 18:00 h. The experimental area had been emersed for approximately 2.5 hours when the first temperature and humidity measurements were taken. Values represent mean ± STD; the number of measurements are in parentheses.

		Time of measurement			
	Height above plates	14:30	15:30	16:30	17:30
Air temperature (°C)	1 cm	16.8 (1)	17.8±0.4 (3)	16.8±0.0 (3)	15.5±0.4 (3)
	1 m	16.4 (1)	16.2 (1)	16.9 (1)	15.3 (1)
Relative humidity (%)	1 cm	78.2 (1)	74.6±3.3 (3)	77.4±1.8 (3)	81.6±2.7 (3)
	1 m	70.5 (1)	63.0 (1)	69.9 (1)	73.4 (1)

are not likely to survive more than four hours of direct exposure to drying conditions occurring in the field at low tide.

4. Vulnerability to predation

Of the 45 species of intertidal invertebrates that were placed in cages with hatchlings, only decapod crustaceans and one fish species caused hatchling mortality (Table III-4). Decapod predators crushed hatchlings, leaving only shell fragments. In separate tests, large *Hemigrapsus nudus* (≥ 29.5 mm carapace width (CW)) or *Cancer productus* (≥ 30 mm CW) would not attack hatchlings. Small *Gobiesox maeandricus* (BL ≤ 47 mm), an intertidal fish, swallowed some hatchlings over the three day period; most of the ingested hatchlings were found alive in translucent fecal sacs, but these hatchlings did not escape from the sacs and died after a few days. Hatchling mortality in cages with other species was similar to that observed in the controls. For *Pisaster ochraceus* (Table III-4), all mortality (four hatchlings) occurred in the cage with the smallest seastar (radial length (R) = 9.8 mm).

5. Predator densities in the field

Of the species that consumed hatchlings in the laboratory (Table III-4), all but four were infrequently observed in areas inhabited by *Nucella emarginata*. However, the total density of hermit crabs (*Pagurus hirsutiusculus*, *P. granosimanus*, and *P. samuelis*) and shore crabs (*Hemigrapsus nudus*) exceeded 400 ind./m^2 at Ross Islets, the most protected of the three sites (Table III-5). Densities of both *P. hirsutiusculus* and *H. nudus* were consistently high at all three sites. Densities of *H. nudus* as high as 360 ind./m^2 were also observed on a nearby islet at Ross Islets in June 1988 (Rawlings, 1990). My observations at several other local sites confirmed that these two predators are abundant at almost all sites, and can even be found among *Mytilus californianus* beds and in tide pools on the open coast. In fact, these results (Table III-5) probably underestimate actual densities since many hermit crabs were in tidepools during low tides and only a few small tidepools were sampled during this study. As the rising tide immersed the intertidal, an

TABLE III-4

Identification of intertidal predators of newly hatched *Nucella emarginata*. Replicate cages contained one animal (potential predator) and 10 hatchlings for three days. Control cages contained only hatchlings. The classification of invertebrates is based on Kozloff (1987).

Species	Size range used in experiments[1]	n[2]	Average # dead or missing hatchlings[3]
CONTROLS		2	0.5
CNIDARIA			
Anthozoa			
1. *Anthopleura elegantissima*	7.9-28.5mm BD	3	0.6
ANNELIDA			
Polychaeta			
2. *Nereis vexillosa*	33-150mm BL	5	0
MOLLUSCA			
Gastropoda			
Prosobranchia			
Archaeogastropoda			
Patellacea			
3. *Lottia digitalis*	7.7-13.5mm SD	3	0
4. *Lottia pelta*	5.8-23.8mm SD	3	0
Trochacea			
5. *Calliostoma ligatum*	6.5-18.9mm SD	3	0.3
6. *Tegula funebralis*	9.6-15.5mm SD	3	0
Mesogastropoda			
7. *Littorina scutulata*	4.8-9.5mm SL	3	0
8. *Littorina sitkana*	3.9-10.3mm SD	3	0
9. *Bittium eschrichtii*	5.0-11.7mm SL	5	0.8

Neogastropoda			
Muricacea			
10. *Ceratostoma foliatum*	12.4-39.6mm SL	3	0
11. *Ocenebra lurida*	3.7-13.3mm SL	3	0.3
12. *Nucella canaliculata*	6.7-26.7mm SL	3	0
13. *Nucella emarginata*	18.2-26.0mm SL	3	0
14. *Nucella lamellosa*	18.5-26.0mm SL	3	0
Buccinacae			
15. *Lirabuccinum (Searlesia) dira*	10.7-32.6mm SL	6	0.5
16. *Alia (Mitrella) gouldi*	4.5-9.5mm SL	3	0.3
17. *Amphissa columbiana*	6.8-22.4mm SL	3	0.6
Opisthobranchia			
Pyramidellacea			
18. *Odostomia sp.*	3.7-6.0mm SL	5	0
Nudibranchia			
19. *Aeolidia papillosa*	9.1-36.2mm BL	3	0
20. *Archidoris montereyensis*	24.3-34.8mm BL	3	0
Gymnomorpha			
21. *Onchidella borealis*	5.1-8.9mm BL	3	0
ARTHROPODA			
Crustacea			
Isopoda			
22. *Cirolana harfordi*	4.3-20.4mm BL	3	0
23. *Gnorimosphaeroma oregonense*	2.7-3.5mm BL	3	0
24. *Idotea wosnesenskii*	16.1-32.5mm BL	5	0
Amphipoda			
25. *Hyale pugettensis*	7.5-12.9mm BL	3	0
Decapoda			
26. *Pagurus granosimanus*	2.9-8.4mm CL	5	5.8
27. *Pagurus hemphili*	5.7-8.5mm CL	3	7.3
28. *Pagurus hirsutiusculus*	4.7-9.4mm CL	3	9.3
29. *Pagurus samuelis*	4.5-5.9mm CL	3	9.3
30. *Oedignathus inermis*	6.9-12.3mm CW	3	9.6
31. *Pachycheles pubescens*	5.5-13.4mm CW	3	0
32. *Petrolisthes cinctipes*	5.6-13.5mm CW	3	0
33. *Pugettia producta*	5.2-13.2mm CW	3	1.0
34. *Pugettia richii*	10.2-15.9mm CW	3	8.6

35. *Cancer productus*	16.5-26.4mm CW	4	8.8
36. *Cancer oregonensis*	13.6-24.7mm CW	3	8.6
37. *Hemigrapsus nudus*	7.7-13.5mm CW	5	7.0
ECHINODERMATA			
Asteroidea			
38. *Dermasterias imbricata*	14.1-26.6mm R	3	0
39. *Henricia leviuscula*	7.4-18.1mm R	3	0
40. *Leptasterias hexactis*	10.0-29.5mm R	5	0.8
41. *Pisaster ochraceus*	9.8-20.0mm R	4	1.5
Holothuroidea			
42. *Cucumaria pseudocurata*	13.5-26.5mm BL	4	0
CHORDATA			
Pisces (intertidal fish)			
43. *Anoplarchus purpurescens*	54-84mm BL	3	0
44. *Gobiesox maeandricus*	39-88mm BL	5	3.2
45. *Oligocottus maculosus*	21-44mm BL	3	0

[1] BD=body diameter, BL=body length, CL=claw length, CW=carapace width, R=radial length, SD=shell diameter, SL=shell length.

[2] n=number of replicates.

[3] Dead or missing hatchlings per cage after three days with predator.

TABLE III-5

Densities of the four main predators of *Nucella emarginata* hatchlings at three field sites. At each site 10 quadrats (25 x 25 cm) were sampled along two 5 m transects set parallel to the shore. The following densities were obtained from counts of predators ≥ the smallest predator capable of killing a 1.2 mm hatchling. Values given are average numbers per m^2 ± STD.

Predator species[1]	Ross Islets	Wizard Islet	Dixon Island
Hemigrapsus nudus	171.2±215.9	67.2±98.9	41.6±42.8
Pagurus hirsutiusculus	225.6±279.0	203.2±172.5	107.2±59.9
P. granosimanus	30.4±57.7	8.0±20.31	0.0±0.0
P. samuelis	11.2±26.2	1.6±5.1	19.2±36.0
Total *Pagurus*	267.2±350.6	212.8±184.5	126.4±85.2
Total predators	438.4±498.3	280.0±242.9	168.0±89.0

[1] The smallest predator sizes, determined using the regression equations between predator claw length (CL) and largest snail killed (chapter VI), are: *H. nudus*: 2.76 mm CL; *P. hirsutiusculus*: 2.31 mm CL; *P. granosimanus*: 2.03 mm CL; *P. samuelis*: 2.31 mm CL.

army of hermit crabs could be seen emerging from tidepools and moist habitats to forage. Other decapods readily consuming hatchlings in the laboratory were generally found at very low densities in areas populated by *N. emarginata*. The intertidal fish *Gobiesox maeandricus* and small individuals of the seastar *Pisaster ochraceus* ($R \leq 40$ mm) were almost exclusively found under rocks and boulders in the low intertidal such that their distribution rarely overlapped with that of *N. emarginata*. The distribution of *G. maeandricus* at high tide, however, is not known.

Discussion

1. Vulnerability to high temperatures

Although most *Nucella emarginata* in Barkley Sound hatch between May and September (appendix 2), which coincides with the time of highest air and surface seawater temperatures, the results of the present study suggest that high temperatures are not likely to be an important direct cause of early juvenile mortality.

Hatchlings located in moist microhabitats could survive the duration of a low tide at temperatures of at least 26 °C (Table III-2), and some hatchlings could even survive at 30 °C. It is probable that most would survive short durations at temperatures of 28-30 °C. Air temperatures in Barkley Sound rarely reach 24 °C, and possibly never exceed 26 °C. Although intertidal substrata exposed to sunlight can become warmer than air, the highest temperatures will only occur for a short time towards the end of the low tide period, and may never exceed 30 °C in Barkley Sound. On 4 August 1993, the warmest day of the year (30.5 °C in Grappler Inlet, only 1 °C cooler than the warmest temperature recorded between 1986 and 1993), air temperature 10 cm above mid-intertidal substrata at Dixon Island only reached 24 °C. Dry rock surfaces exposed to the sun at ≈2.1 m above MLLW, near the upper limit of *N. emarginata* distribution at that site, reached 28.5 °C at 12:30 h (≈30 minutes before being immersed by the incoming tide). At that time, the temperature of shaded rock surfaces only reached 22 °C.

Surface seawater temperature never exceeded 20 °C and is probably not a direct cause of mortality in Barkley Sound, as most hatchlings and adults can survive at least eight hours of immersion in seawater at 30 °C.

Previous studies of late juvenile or adult invertebrates have concluded that maximum temperatures on temperate rocky shores were below lethal levels (Davies, 1969; Wolcott, 1973; Underwood, 1979). The present study suggests that the same is true for early juveniles, even though early juveniles may be more vulnerable than adults. High temperatures may nevertheless be an indirect cause of mortality by increasing evaporation rates (Wolcott, 1973), and thus mortality by desiccation.

2. Vulnerability to desiccation

Early juvenile *Nucella emarginata* are not likely to survive direct exposure to intense or even moderate drying conditions for the duration of a low tide. In both field and laboratory desiccation experiments hatchlings started dying shortly after the substratum dried, and no hatchling survived six hours of emersion. The absence of mortality in the 26 °C treatment of the high temperature experiment confirms that mortality in the desiccation experiments was indeed caused by desiccation rather than heat stress. Microhabitats that dry out even for short periods during low tides may prove lethal. But while desiccation conditions in the field can be a serious threat to early juveniles, they will rarely be lethal for healthy adults. Vulnerability to desiccation also decreases with increasing size in barnacles (Foster, 1971), limpets (Wolcott, 1973; Branch, 1975), and other snails (Berry and Hunt, 1980; Garrity, 1984).

Relative humidity in the intertidal zone probably remains higher at the surface of intertidal substrata than in surrounding air (Table III-3). Nevertheless, near-surface humidity levels, in combination with air circulation, are low enough to produce substantial desiccation of intertidal substrata and organisms as was often evidenced by the dry, brittle fronds of macroalgae at low tide. Humidity levels at the surface of mid-intertidal substrata in Barkley Sound can reach levels that would result in 100% mortality of exposed hatchling *N. emarginata*.

3. Vulnerability to predation

Contrary to the suggestion by Thorson (1966) that small juvenile invertebrates will be preyed upon by a wide variety of predators, few species killed newly hatched *Nucella emarginata*. Laboratory experiments suggest that decapod crustaceans are the only important predators of hatchlings in Barkley Sound. These species, however, are abundant and could exact a heavy toll on young cohorts.

Decapod predators do consume hatchlings in the field, as shell fragments are regularly found in samples of filamentous algae and mussel clusters (pers. obs.). Hermit crabs, especially *P. hirsutiusculus*, are active foragers and are often active even at low tide until the surfaces dry out. In addition, they are often found "sitting" on clutches of ripe egg capsules (unpubl. data), possibly feeding on the young snails as they emerge from the capsules. In the laboratory, *P. hirsutiusculus* rapidly finds and consumes all *N. emarginata* hatchlings (this study) and will also feed on hatchlings of a variety of other gastropod species (Spight, 1976; Rivest, 1983). It is often the most abundant and is probably the most important predator of early juvenile *N. emarginata* and other small gastropods at most field sites.

Some *Hemigrapsus nudus* never attacked hatchlings in the laboratory trials, and uneaten snails were left in most cages after three days with a crab. According to Knudsen (1964), *H. nudus* feeds mainly on plant material and occasionally consumes animal tissue. *H. nudus* will, however, feed on littorines (Boulding and Van Alstyne, 1993) and on *N. emarginata* egg capsules in the field (Rawlings, 1990). Although hatchlings are probably not a preferred food item of *H. nudus*, this predator may nevertheless be responsible for a significant portion of hatchling mortality given its high densities among habitats colonized by *N. emarginata*.

None of the grazers or other herbivores caused hatchling mortality. Birds, which were reported to consume small *Nucella lapillus* on British shores (Feare, 1970), were not observed feeding on *N. emarginata*. Levels of predation by pelagic fish are unknown.

Hatchling and adult *N. emarginata* have distinct sets of predators. In separate trials (chapter VI), the largest *P. hirsutiusculus* (claw length (CL) = 14.0 mm) never killed or damaged adult snails. The largest *H. nudus* to attack snails (CL = 21.1 mm) could kill small adults (≤17 mm shell length), but this was infrequent even when crabs and snails were confined to the same cage for several days, and such large *H. nudus* have not been observed in *N. emarginata* habitats (chapter VI). Predators of adult *N. emarginata*, large *Pisaster ochraceus* (R ≈ 40 mm or larger) and *Cancer productus* (CW ≈ 40 mm or larger), never killed hatchlings.

Shell-crushing predators have been identified as selective agents influencing the morphology of gastropod shells (in Vermeij, 1978, 1987, 1993; Crothers, 1985; Faller-Fritsch and Emson, 1985; Palmer, 1985). The results of this study show that shell-crushing predators can be the only predators of gastropods at the onset of independent benthic life. In *N. emarginata*, predators that do not damage the shell, such as seastars, become important later in life. Structural features that increase resistance to shell-crushing predators could therefore have a greater effect on survival during the vulnerable early juvenile period than at any time later in life. Yet, shell spines, ribs, varices, and teeth are usually absent or minimal in very young snails, but are most developed in mature individuals (Vermeij, 1987, 1993). Rapid growth is often considered to be an important strategy used by young organisms to reduce mortality to predation (Vermeij, 1987; Werner and Gilliam, 1984). Growth, however, does not solve the immediate problem of high vulnerability. Other features, such as initial shell size, shape, and thickness could be important elements of the adaptive response to predators of early juvenile gastropods (Spight, 1976; Rivest, 1983). Nevertheless, all newly-hatched *N. emarginata* remain vulnerable to abundant predators and to desiccation conditions at low tide; use of microhabitats which offer protection from these mortality factors may be the single most important means of surviving through the early juvenile period (chapter IV).

4. Other factors

Other potential causes of mortality include dislodgement by waves, carrying hatchlings away from suitable habitats, and crushing by water-borne debris. In laboratory observations (chapter IV), hatchlings were able to remain attached and even crawl on a rock surface when exposed to moderately high levels of turbulence (flow velocities up to ≈15 cm/second). Consequently, waves and water currents might cause little mortality on protected or moderately wave-exposed shores. However, dislodgement by waves could be important at sites exposed to strong wave action if the hatchling is exposed to the full impact of the waves during incoming or receding tides. Hatchling *N. emarginata* are probably most vulnerable to dislodgement when they emerge and crawl off their egg capsule, which is flexible and may provide poor footing in turbulent conditions. They were never observed emerging at low tide, however, and were infrequently found on or at the base of the egg capsules when the tide was out. This suggests that individuals within the capsules may be able to recognize conditions that indicate the tide is receding and consequently stop emerging some time before the water surface reaches the capsules.

During laboratory experiments (chapter II), approximately 15% of newly hatched *N. emarginata* died of unknown causes during the first 30 days after hatching; these snails had been continuously immersed in flowing seawater, provided with food, and no predators were present. Under similar conditions, 69.6% of recently hatched *Searlesia dira*, a prosobranch gastropod, died over a period of 36 days (Rivest, 1983). Diseases, parasites, damage due to ultraviolet radiation, and complications arising during metamorphosis may cause substantial early juvenile mortality. Little information is available on the occurrence of these factors in intertidal organisms.

5. Conclusion

Desiccation and predation by decapod crustaceans (*Pagurus* and *Hemigrapsus*) appear to be the most significant threats to early juvenile *Nucella emarginata*. At sites exposed to intense wave action, dislodgement by waves may also become an important factor. These factors, particularly desiccation, are prevalent on most temperate rocky intertidal shores. When intertidal invertebrates with motile early juveniles hatch or settle and begin to explore their new habitat, they are directly exposed to these factors. In newly hatched *N. emarginata*, these factors can cause 100% mortality of early juveniles that are not protected from their effects. Consequently, desiccation and predation by decapod predators undoubtedly exert considerable selective pressures on intertidal invertebrate populations, shaping life history strategies and early juvenile traits, such as timing of settlement or hatching relative to the tidal cycle and microhabitat preferences.

References

Bachelet, G. 1989. Recruitment in *Albra tenuis* (Montagu) (Bivalvia, Semelidae), a species with direct development and a protracted meiobenthic phase. In: Reproduction, Genetics and Distributions of Marine Organisms. Proc. 23rd Europ. Mar. Biol. Symp. Eds. J.S. Ryland and P.A. Tyler. Olsen and Olsen, Fredensborg, Denmark. pp. 23-30.

Barnes, H. and H.T. Powell. 1950. The development, general morphology and subsequent elimination of barnacle populations, *Balanus crenatus* and *B. balanoides*, after a heavy initial settlement. J. Anim. Ecol. 19: 175-179.

Benedetti-Cecchi, L. and F. Cinelli. 1992. Effects of canopy cover, herbivores and substratum type on patterns of *Cystoseira* spp. settlement and recruitment in littoral rockpools. Mar. Ecol. Prog. Ser. 90: 183-191.

Bergeron, P. and E. Bourget. 1986. Shore topography and spatial partitioning of crevice refuges by sessile epibenthos in an ice disturbed environment. Mar. Ecol. Prog. Ser. 28: 129-145.

Berry, A.J. and D.C. Hunt. 1980. Behaviour and tolerance of salinity and temperature in new-born *Littorina rudis* (Maton) and the range of the species in the Forth Estuary. J. Moll. Stud. 46: 55-65.

Bertness, M.D. 1989. Intraspecific competition and facilitation in a northern acorn barnacle population. Ecology. 70: 257-268.

Blegvad, H. 1929. Mortality among animals of the littoral region in ice winters. Rep. Danish Biol. Stat. XXXV. pp. 51-62.

Boulding, E.G. and K.L. Van Alstyne. 1993. Mechanisms of differential survival and growth of two species of *Littorina* on wave-exposed and on protected shores. J. Exp. Mar. Biol. Ecol. 169: 139-166.

Branch, G.M. 1975. Ecology of *Patella* species from the Cape Peninsula, South Africa. IV. Desiccation. Mar. Biol. 32: 179-188.

Brawley, S.H. and L.E. Johnson. 1991. Survival of fucoid embryos in the intertidal zone depends on developmental stage and microhabitat. J. Phycol. 27: 179-186.

Connell, J.H. 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. Ecol. Monogr. 31: 61-104.

Connell, J.H. 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. Ecol. Monogr. 40: 49-78.

Crothers, J.H. 1985. Dogwhelks: an introduction to the biology of *Nucella lapillus* (L.). Field Studies. 6: 291-360.

Davies, P.S. 1969. Physiological ecology of *Patella*. III. Desiccation effects. J. Mar. Biol. Ass. U.K. 49: 291-304.

Day, R.W., A. Barkai, and P.A. Wickens. 1991. Trapping of three drilling whelks by two species of mussel. J. Exp. Mar Biol. Ecol. 149: 109-122.

Dayton, P.K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41: 351-389.

Denley, E.J. and A.J. Underwood. 1979. Experiments on factors influencing settlement, survival, and growth of two species of barnacles in New South Wales. J. Exp. Mar. Biol. Ecol. 36: 269-293.

Dittman, D. and C. Robles. 1991. Effect of algal epiphytes on the mussel *Mytilus californianus*. Ecology. 72: 286-296.

Faller-Fritsch, R.J. and R.H. Emson. 1985. Causes and patterns of mortality in *Littorina rudis* (Maton) in relation to interspecific variation: a review. In: The Ecology of Rocky Coasts: Essays Presented to J.R. Lewis. Eds. P.G. Moore and R. Seed, Hodder and Stoughton, London. pp. 157-177.

Feare, C.J. 1970. Aspects of the ecology of an exposed shore population of dogwhelks *Nucella lapillus* (L.). Oecologia. 5: 1-18.

Fernandez, M., O. Iribarne, and D. Armstrong. 1993. Habitat selection by young-of-the-year Dungeness crab *Cancer magister* and predation risk in intertidal habitats. Mar. Ecol. Prog. Ser. 92: 171-177.

Fletcher, W.J. and A.J. Underwood. 1987. Interspecific competition among subtidal limpets: effect of substratum heterogeneity. Ecology. 68: 387-400.

Foster, B.A. 1971. Desiccation as a factor in the intertidal zonation of barnacles. Mar. Biol. 8: 12-29.

Garrity, S.D. 1984. Some adaptations of gastropods to physical stress on a tropical rocky shore. Ecology. 65: 559-574.

Gosselin, L.A. and P.-Y. Qian. Submitted. Early postsettlement mortality of an intertidal barnacle: a critical period for survival. Ecology.

Jablonski, D., and R.A. Lutz. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. Biol. Rev. 58: 21-89.

Keesing, J.K. and A.R. Halford. 1992. Field measurement of survival rates of juvenile *Acanthaster planci*: techniques and preliminary results. Mar. Ecol. Prog. Ser. 85: 107-114.

Knudsen, J.W. 1964. Observations of the reproductive cycles and ecology of the common Brachyura and crablike Anomura of Puget Sound, Washington. Pacif. Sci. 18: 3-33.

Kozloff, E.N. 1987. Marine invertebrates of the Pacific northwest. University of Washington Press, Seattle, WA. 511 pp.

Miller, K.M. and T.H. Carefoot. 1989. The role of spatial and size refuges in the interaction between juvenile barnacles and grazing limpets. J. Exp. Mar. Biol. Ecol. 134: 157-174.

Orensanz, J.M. and V.F. Galluci. 1988. Comparative study of postlarval life-history schedules in four sympatric species of *Cancer* (Decapoda: Brachyura: Cancridae). J. Crust. Biol. 8: 187-220.

Osman, R.W., R.B. Whitlach, and R.J. Malatesta. 1992. Potential role of micro-predators in determining recruitment into a marine community. Mar. Ecol. Prog. Ser. 83: 35-43.

Paine, R.T. 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15: 93-120.

Paine, R.T. 1976. Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. Ecology. 57: 858-873.

Palmer, A.R. 1985. Adaptive value of shell variation in *Thais lamellosa*: effect of thick shells on vulnerability to and preference by crabs. Veliger. 27: 349-356.

Palmer, A.R., S.D. Gayron, and D.S. Woodruff. 1990. Reproductive, morphological, and genetic evidence for two cryptic species of Northeastern Pacific *Nucella*. Veliger. 33: 325-338.

Petraitis, P.S. 1983. Grazing patterns of the periwinkle and their effects on sessile intertidal organisms. Ecology 64: 522-533.

Petraitis, P.S. 1987. Immobilization of the predatory gastropod, *Nucella lapillus*, by its prey, *Mytilus edulis*. Biol. Bull. 172: 307-314.

Rawlings, T.A. 1990. Associations between egg capsule morphology and predation among populations of the marine gastropod, *Nucella emarginata*. Biol. Bull. 179: 312-325.

Rivest, B.R. 1983. Development and influence of nurse egg allotment on hatching size in *Searlesia dira* (Reeve, 1846) (Prosobranchia: Buccinidae). J. Exp. Mar. Biol. Ecol. 69: 217-241.

Robertson, A. 1991. Effects of a toxic algal bloom of *Chrysochromulina polylepis* on the common dog-whelk, *Nucella lapillus*, on the Swedish west coast. J. Mar. Biol. Ass. U.K. 71: 569-578.

Sarver, D.J. 1979. Recruitment and juvenile survival in the sea hare *Aplysia juliana* (Gastropoda: Opisthobranchia). Mar. Biol. 54: 353-361.

Spight, T.M. 1976. Ecology of hatching size for marine snails. Oecologia. 24: 283-294.

Thorson, G. 1966. Some factors influencing the recruitment and establishment of marine benthic communities. Neth. J. Sea Res. 3: 267-293.

Underwood, A.J. 1979. The ecology of intertidal gastropods. Adv. Mar. Biol. 16: 111-210.

Vadas, R.L., W.A. Wright, and S.L. Miller. 1990. Recruitment of *Ascophyllum nodosum*: wave action as a source of mortality. Mar. Ecol. Prog. Ser. 61: 263-272.

Vermeij, G.J. 1972. Intraspecific shore-level size gradients in intertidal molluscs. Ecology. 53: 693-700.

Vermeij, G.J. 1978. Biogeography and Adaptation. Patterns of Marine Life. Harvard University Press, Cambridge, Massachussetts, USA. 332 p.

Vermeij, G.J. 1987. Evolution and Escalation. An Ecological History of Life. Princeton University Press, Princeton, New Jersey, USA. 527 p.

Vermeij, G.J. 1993. A Natural History of Shells. Princeton University Press, Princeton, New Jersey, USA. 207 p.

Werner, E.E. and J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst. 15: 393-425.

Wethey, D.S. 1985. Catastrophe, extinction, and species diversity: a rocky intertidal example. Ecology. 66: 445-456.

Wolcott, T.G. 1973. Physiological ecology and intertidal zonation in limpets (*Acmaea*): a critical look at "limiting factors". Biol. Bull. 145: 389-422.

Young, B.L. 1991. *Spartina* axil zones: preferred settlement sites of barnacles. J. Exp. Mar. Biol. Ecol. 151: 71-82.

Young, C.M. and F.-S. Chia. 1984. Microhabitat-associated variability in survival and growth of subtidal solitary ascidians during the first 21 days after settlement. Mar. Biol. 81: 61-68.

CHAPTER IV

Distribution and dispersal of early juvenile snails in the intertidal zone: significance of microhabitat use in newly hatched *Nucella emarginata*.

Introduction

Although most aquatic organisms are highly vulnerable to mortality factors during the early juvenile period (Werner and Gilliam, 1984; chapter III), actual levels of juvenile mortality are often dependant on microhabitat use. In lakes and streams, juvenile fish are often located in aquatic vegetation in which they suffer lower mortality by predation than in open water (Werner et al., 1983; Mittelbach, 1984; Werner and Hall, 1988). In subtidal marine habitats, juvenile lobsters are associated with cobble and algae, which effectively reduce predation risk (Herrnkind and Butler, 1986; Smith and Herrnkind, 1992; Wahle and Steneck, 1992). Most studies of microhabitat use by motile early juvenile aquatic animals have examined freshwater or subtidal marine organisms, and assumed predation to be the single most important cause of mortality. Inhabitants of the rocky intertidal zone are exposed to predators, but also to factors that do not occur in subtidal habitats or in most freshwater habitats, such as desiccation and pronounced variations in temperature (chapter III), and to wave action, which is most intense in the intertidal zone. Desiccation is of particular interest because it is often the most severe and possibly the most widespread mortality factor in rocky intertidal habitats, and often the physical factor most likely to cause mortality (Underwood, 1979; chapter III). However, the effectiveness of rocky intertidal microhabitats as shelters from desiccation or predation for motile early juveniles has not been examined.

Since vulnerability generally scales inversely with body size, rapid growth during the early juvenile period is also considered to be an important strategy to reduce the likelihood of mortality by minimizing the time spent in the smallest, most vulnerable size classes (Vermeij, 1978, 1987). If rapid growth is a priority, early juveniles should use microhabitats that offer the most favorable growth conditions. Hence, the distribution of motile early juveniles would be expected to correspond to food distribution, either in terms of abundance or value of food items to the juvenile.

The study of distribution and microhabitat use by early juvenile intertidal organisms can be difficult because early juveniles are often available only during a brief period as a result of seasonal spawning, and the exact time of their availability may be unpredictable. Due to an extended spawning season, however, newly hatched *Nucella emarginata* (Deshayes) (northern) (cf. Palmer et al., 1990), an intertidal muricid gastropod, are available in the field for at least 3 to 7 months of the year (Spight, 1982; appendix 2). This gastropod has an extended geographic range along the northwestern coast of North America (Palmer, 1984, 1985) and is often one of the most abundant gastropods in rocky intertidal habitats. In addition, early juvenile *N. emarginata* are relatively undisturbed by gentle handling (appendix 1). The distribution of early juvenile *N. emarginata* in the field has not been determined, but hatchlings of an Atlantic species, *Nucella lapillus*, have been found on the underside of rocks (Moore, 1938) and in empty barnacle shells, but not on open rock surfaces (Feare, 1970), suggesting a non-random distribution. Although newly hatched *N. emarginata* are most vulnerable to desiccation and predation by decapod crustaceans (chapter III) and are unable to grow on energy reserves remaining from the egg capsule (chapter II), it is not known whether the provision of shelter from mortality factors or the distribution of prey are important determinants of the distribution of early juveniles among microhabitats.

In muricid gastropods that hatch from benthic egg capsules as crawl-away juveniles, it is generally assumed that individuals remain within a short distance of the hatching site throughout their life (Spight, 1974; Crothers, 1985), and that effects of most passive mechanisms of gene flow are probably minimal (Palmer, 1984). Populations of these snails are believed to be mostly restricted to small areas of the shoreline (Spight, 1974, 1975), and deep water or protected bays and inlets are expected to act as barriers to gene flow (Palmer, 1984). These assumptions, however, are mostly based on studies of late juvenile and adult snails. The dispersal capabilities of small, newly hatched muricids have never been established. Yet, certain benthic marine invertebrates lacking a planktonic larval stage, such as bivalves, seastars, and snails, can disperse in the water column when very small (Sellmer, 1967; Booth, 1979; Martel and Chia, 1991a). In fact, some molluscs actively initiate this mode of dispersal by raising their foot, releasing hold of the substratum, and producing mucous or byssal threads, allowing them to become suspended in currents and turbulent water and thus drift to new sites (Sorlin, 1988; Martel and Chia, 1991b). Recently, two hatchling *N. emarginata* were caught in collectors suspended in the intertidal zone by Martel and Chia (1991a), who also reported that these hatchlings produced mucus threads which considerably reduced sinking rates. Their results suggest that newly hatched *N. emarginata* may disperse by drifting in the water column. If so, this would have important implications regarding access to microhabitats, since dispersal capabilities determine which microhabitats are within reach and how long it will take to get to a given microhabitat, but also in regards to current assumptions on population size and range.

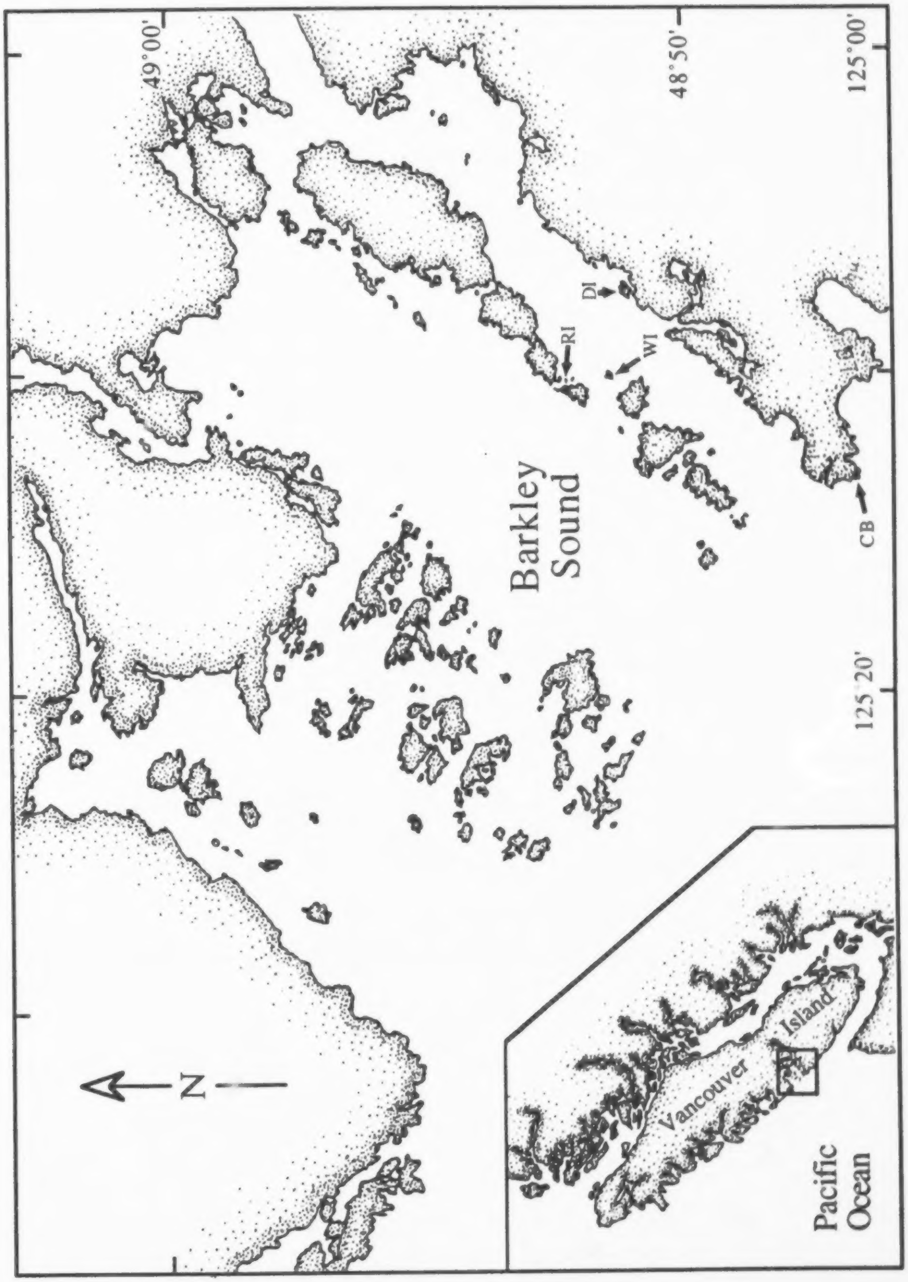
The objectives of this study were therefore to: 1) identify the microhabitats used by early juvenile *N. emarginata* in the field; 2) examine the significance of microhabitat use by hatchlings in terms of protection from the main threats to survival (predation and desiccation) and in terms of prey availability; and 3) determine how *N. emarginata* disperse after emerging from their egg capsule, and examine the implications of mode of dispersal for access to microhabitats during the early juvenile period and for population parameters.

Materials and methods

1. Study site and organism

Laboratory experiments were carried out at the Bamfield Marine Station; field collections, observations and experiments were made at nearby intertidal sites in Barkley Sound (Fig. IV-1). Newly hatched *Nucella emarginata* used in the experiments described below were obtained by collecting ripe egg capsules (egg capsules that are unplugged but still contain fully developed snails that have not yet emerged) from Dixon Island (48°51'15" N, 125°06'90" W) and Wizard Islet (48°51'45" N, 125°09'55" W) (Fig. IV-1).

Figure IV-1. Map of Barkley Sound showing study sites. CB = Cape Beale, DI = Dixon Island, RI = Ross Islets, WI = Wizard Islet.


49°00'
48°50'
125°00'
125°20'
Barkley Sound
RI
DI
WI
CB
N
Vancouver Island
Pacific Ocean

2. Distribution in the field

The use of structurally complex microhabitats by *Nucella emarginata* throughout ontogeny was examined by sampling populations at three sites (Fig. IV-1): Ross Islets (48°52'35" N, 125°09'65" W), a site protected from wave action, was sampled in July 1992 and again in September 1993; Wizard Islet, exposed to moderate wave action, was sampled in September 1991 and in August 1992; Cape Beale (48°47'20" N, 125°12'95" W), exposed to full ocean surge, was sampled once in July 1992. For each sampling, quadrats (25 x 25 cm) were positioned at one meter intervals along transects running parallel to the shore in areas populated by *N. emarginata*. Sampling was carried out when hatchlings and juveniles were known to be present (appendix 2). For each quadrat, the first step of the sampling procedure was to closely examine the enclosed area and collect all snails found on open surfaces. These observations were carried out without disturbing the habitat except for the careful displacement or removal of fucoid algae, when present. Hatchlings were not found on fucoid fronds or holdfasts in preliminary samples or throughout the study; late juveniles and adults were very rarely attached to fucoid algae. In addition, fucoid fronds are raised at high tide and do not constitute shelter from crabs and hermit crabs, the main predators of *N. emarginata* hatchlings (chapter III). The second step consisted of collecting the structurally complex microhabitats within the same quadrat. At Ross and Wizard, this mainly consisted of mussel clusters (*Mytilus californianus* and *M. trossulus*), barnacles (mostly *Semibalanus cariosus*), and tufts of the filamentous algae *Cladophora columbiana*. At Cape Beale, *M. californianus*, *S. cariosus*, and the gooseneck barnacle *Pollicipes polymerus* were collected; *C. columbiana* was absent except for a few tufts in protected crevices. When little of these microhabitats were present within a quadrat, all was collected. Often, however, a subsample of each microhabitat was collected for a total volume of ≈0.75 - 1 litre. Samples were then returned to the laboratory and thoroughly washed in fresh water to extract all snails from the microhabitats. Snails ≤3 mm were measured using the ocular micrometer of a dissecting microscope (± 0.039 mm); larger individuals were measured using a dial caliper

(± 0.1 mm). The size and position of each snail, either on open surfaces or hidden with structurally complex microhabitats, was recorded.

3. Effectiveness of microhabitats as shelters

Because small *Nucella emarginata* were found almost exclusively within *Cladophora columbiana*, mussel clusters, or dense assemblages of the barnacle *Semibalanus cariosus*, the effectiveness of these microhabitats as shelters from desiccation and predation was examined. Each microhabitat was reproduced on 8 x 8 x 1 cm shale rock plates, three replicate plates per microhabitat. The algae, mussels, and barnacle shells collected from the field to build the microhabitat plates were initially washed in freshwater to remove all snails that might be present. The plates were then prepared so as to simulate as closely as possible the microhabitats as they occur in the field, as follows.

Cladophora plates: tufts of *Cladophora columbiana* were sewn onto the plates using 6 lb. monofilament line. The surface of each plate was thus covered by a dense mat of *Cladophora* with strands 5 - 6 cm high. *Cladophora* tufts were removed after each experimental run to recover the hatchlings; the three plates were then prepared again with new tufts for each run.

Barnacle plates: large shells of *Semibalanus cariosus* (11 - 34 mm basal diameter, 20 - 40 mm height) were attached in dense assemblages to each rock plate. Many of the shells were collected from dead barnacles, as live barnacles were inevitably killed when detached from intertidal rock surfaces. These large shells, however, supported many smaller barnacles (*S. cariosus*, *Balanus glandula*, and *Chthamalus dalli*), and care was taken to ensure that these stayed alive throughout the study. The body cavity of the large barnacles was cleaned, the operculum was plugged with hot melt glue and the base was levelled with sandpaper before being attached to the plate using epoxy glue. One or two large shells on each plate were left unplugged to simulate dead barnacles. Once prepared, these plates were placed in flowing seawater for two weeks before being used in experiments. After each experimental run, hatchlings were recovered by washing and spraying the shells with freshwater. The same plates were used in all experiments.

Mussel plates: live *Mytilus trossulus* and *M. californianus* (5 - 65 mm shell length) were placed on the rock plates in seawater for eight days during which they attached to the plates and to each other with byssal threads. During this period water flow was gradually increased, stimulating mussels to attach more strongly by producing more byssal threads. The resulting mussel clusters covered the plates with a layer of 4 - 5 cm depth. The clusters were detached after each run to recover the hatchlings, and new plates were prepared again for subsequent runs.

Open surface plates: a set of three bare plates was also included in each experimental run. These plates were placed in tanks with flowing seawater for two weeks prior to experimentation to allow the formation of a biofilm on the plate surfaces, as this might affect water retention and snail behaviour.

3.1 Protection from desiccation

The effectiveness of these four microhabitats as shelters from desiccation was determined in a field experiment at Wizard Islet on 11 September 1993. On that day, sunny, windy conditions coincided with an afternoon low tide, exposing intertidal organisms to high desiccation stress. Before leaving for the field, 8 - 10 day old hatchlings were inserted in the microhabitats, 20 hatchlings per plate. The plates were immersed in seawater for 45 minutes to allow the hatchlings to attach and crawl to a desired position. All plates were then placed in sealed containers and brought to the field. Open surface plates did not receive hatchlings until reaching the field site. Once in the field, the open surface plates were put in a tray with seawater and 20 hatchlings were placed on each plate. When these hatchlings had attached, the plates were gently removed from the water. All 12 plates (3 replicates x 4 microhabitats) were then placed on a large mat (≈0.75 x 1 m) of *Cladophora columbiana* growing on an area of flat, horizontal rock in the intertidal zone. The contact between the plates and the seawater absorbed in the *Cladophora* mat helped maintain the plates at a temperature similar to that of nearby substrata. The site was approximately 1.8 m above mean lower low water

(MLLW), in an area supporting *N. emarginata* snails and egg capsules. After four hours the plates were returned to the laboratory. Hatchlings were recovered from the microhabitats and placed in flowing seawater for 24 hours. Each snail was then examined under a dissecting microscope; snails not responding when the operculum was touched with a probe were recorded as dead.

3.2 Protection from predators

The effectiveness of hatchling microhabitats as shelters from hermit crabs (*Pagurus* spp.) and shore crabs (*Hemigrapsus nudus*), the main predators of hatchlings (chapter III), was examined in the laboratory. Each plate was placed in a cage slightly larger than the plate itself (modified food containers, 9.5 x 9.5 x 6 cm, with 610 μm mesh screening). In preliminary trials, some hatchlings on the open surface plates crawled to the sides or under the plates; this treatment was therefore carried out without rock plates, the snails being placed directly on bottom of the cage. Twenty hatchlings were added to each microhabitat, after which the sealed cages were immersed in seawater for 45 minutes before adding the predators. Each cage then received one *Pagurus hirsutiusculus* (5 - 6 mm claw length (CL)), one *P. granosimanus* (5 - 6 mm CL) and one *H. nudus* (6 - 7 mm CL). The cages were then placed in a 250 litre O-shaped "surge tank" (length = 170 cm, width = 65 cm, height = 40 cm) equipped with an electric motor attached to a paddle providing a continuous back and forth water motion to simulate hydrodynamic conditions in the intertidal zone at high tide. The surge-inducing paddle completed ≈5.5 back-and-forth cycles per minute, producing reversing water flows ranging in velocity from 0 to ≈15 cm / second. Cages were removed after five hours and the contents were carefully examined for hatchlings and shell fragments. This experiment was carried out twice in July 1993, for a total sample size of six replicates per microhabitat.

4. Distribution of prey

To determine if early juvenile *Nucella emarginata* use microhabitats containing the best supply of prey, I examined the distribution of species previously identified as hatchling prey (chapter II) among the microhabitats used by hatchlings. On 12 - 15

August 1993, samples were collected at Dixon Island and Wizard Islet; each microhabitat was abundant at these sites, allowing comparisons of microhabitat-specific prey densities. At each site, five quadrats (5 x 5 cm) haphazardly positioned over patches of each microhabitat were sampled. Prey present on open rock surfaces were counted on location. For *Cladophora*, mussel, and *Semibalanus* microhabitats, contents of the quadrats were collected and examined in the laboratory. Given the preference of hatchlings for very small *Mytilus* spp. (chapter V), counts of *Mytilus* spp. were subdivided into two shell length size classes: 0.5 - 5 mm, and 5.1 - 10 mm. *Mytilus* spp. >10 mm and *Balanus glandula* >8 mm basal diameter were not counted because hatchlings are often unable to successfully attack such large prey (Palmer, 1990; pers. obs.).

5. Dispersal of hatchlings

5.1 Dispersal in the water column

The prevalence of dispersal in the water column was examined in the field by quantifying recruitment to a collector (modified from Martel and Chia, 1991a) mimicking two microhabitats commonly used by newly hatched *N. emarginata*. The collector (Fig. IV-2) consisted of a 2.54 cm PVC plastic tubing frame supporting two pouches (15 x 15 cm, and 2 - 5 cm thick) of 4.5 mm mesh screen at a height of 15 cm above the substratum. One pouch was filled with mussels (*M. trossulus* and *M. californianus*, size range = 2 - 50 mm shell length) that had been washed in freshwater, packed into the pouch, and placed in flowing seawater for three days to allow the production of new byssal threads. The other pouch was filled with *Cladophora columbiana* and three small rocks, enclosed to lend support and prevent the pouch from collapsing on the algae. The pouches were then tightly attached to the frame. To prevent snails from crawling up to the pouches from the substratum, copper wires (≈3 mm diameter) were wrapped around each base of the frame to produce bands of copper 2.1 cm wide. The holders in which the collector would be inserted were cemented to the rock using Z-SPAR® splash zone epoxy. The collector was installed at the seaward entrance of a surge channel at Dixon Island on 17 August, 6 September, and 11 September 1993. On each occasion, the

Figure IV-2. Collector installed in surge channel at Dixon Island, July 1993.

collector was recovered after 48 hours and the content of each pouch was washed in freshwater. This channel was densely populated by *N. emarginata*; hatchlings had been emerging from egg capsules in the channel since early July and continued to hatch throughout the study period (appendix 2). Surface water conditions were moderately turbulent on each occasion.

5.2 Crawling speed

Crawling speed of *Nucella emarginata* emerging from their egg capsule was examined in the laboratory. Hatchlings were never directly handled before or during the experiment. Ripe egg capsules collected at Dixon Island were fastened by their base in a small hole at the center of a large shale rock plate (35 x 35 x 1 cm) which was placed upright in the surge tank parallel to the water flow. Water flow conditions were the same as in the predation experiment. Movements of all hatchlings that emerged and crawled onto the vertical rock surface during a three hour period were recorded on video tape. When the recordings were subsequently viewed, the position of each hatchling during the first 30 minutes after it crawled off the egg capsule was marked on acetate transparencies at one minute intervals. These positions were then digitized using a Summagraphics® digitizing tablet connected to a MacIntosh® computer, allowing accurate calculations of crawling speed.

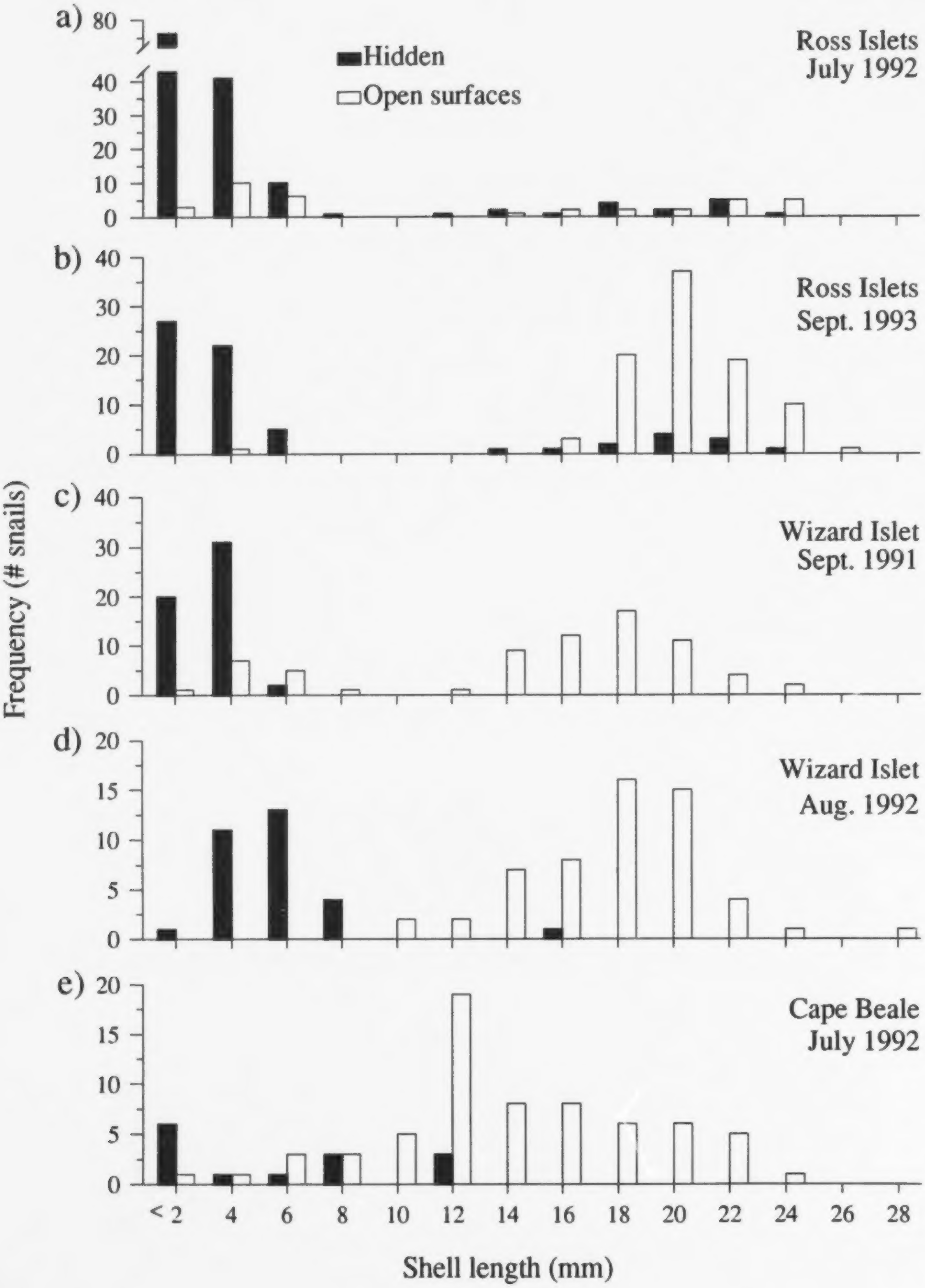
Results

1. Distribution in the field

For each site and year sampled, the distribution of *Nucella emarginata* changed considerably as a function of body size (Fig. IV-3). Large individuals were mostly on open surfaces, while small *N. emarginata* were hidden within structurally complex micro-habitats.

A close examination of several microhabitats revealed that snails ≤4 mm were almost exclusively located in the filamentous algae *Cladophora*, in mussel clusters (*Mytilus* spp.), and among dense assemblages of large *Semibalanus cariosus*. Snails ≤4 mm were not found on fronds or holdfasts of fucoid algae or in filamentous algae other

Figure IV-3. Size distribution of *Nucella emarginata* on open surfaces or hidden in structurally complex microhabitats (filamentous algae, mussel clusters, and assemblages of large barnacles). Snails and microhabitats were sampled within 25 x 25 cm quadrats at 1 m intervals along transects running parallel to the shore. Sites were selected along a gradient of wave exposure: protected - Ross Islets: a) 10 quadrats, b) 10 quadrats; moderate exposure -Wizard Islet: c) 20 quadrats, d) 20 quadrats; full exposure to ocean surge -Cape Beale: e) 14 quadrats.


a)
80
40
30
20
10
0
■Hidden
□Open surfaces
Ross Islets
July 1992
b)
40
30
20
10
0
Ross Islets
Sept. 1993
c)
40
30
20
10
0
Wizard Islet
Sept. 1991
d)
20
15
10
5
0
Wizard Islet
Aug. 1992
e)
20
15
10
5
0
Cape Beale
July 1992
< 2
4
6
8
10
12
14
16
18
20
22
24
26
28
Frequency (# snails)
Shell length (mm)

than *C. columbiana*, and they were rarely found among small barnacles (*B. glandula*, *C. dalli*, and small *S. cariosus*). Narrow cracks and crevices and the undersides of rocks and boulders were also examined, but these did not contain small *N. emarginata*.

Snail sizes were not distributed evenly among the three microhabitats in which juveniles were found (Fig. IV-4). The size-frequency distribution of snails in mussel clusters was not significantly different from that of snails among *Semibalanus* ($G = 5.39$, $p > 0.99$, $df = 18$; R x C unplanned test of homogeneity, Sokal and Rohlf, 1981). When size-frequencies of snails in *Cladophora* were included in the analysis, however, the test was highly significant ($G = 110.2$, $p < 0.0001$, $df = 18$) indicating that the size-frequency distribution of juveniles in *Cladophora* was more skewed towards the smallest size classes. Almost all snails in *Cladophora* tufts were ≤ 3.5 mm in shell length, while mussel clusters and *Semibalanus* contained juveniles of all sizes (Fig. IV-4).

Comparisons of total snail densities between microhabitats were not possible because unequal subsamples of each microhabitat were collected, and because quadrats rarely contained all microhabitats, an essential requirement for such comparisons due to the limited dispersal capability of hatchlings. Casual observations suggested that the abundance of hatchlings within a microhabitat sample was highest in the proximity of egg capsules from which hatchlings had recently emerged.

2. Effectiveness of microhabitats as shelters

2.1 Protection from desiccation

When exposed to drying conditions in the intertidal for four hours, mortality of hatchlings hidden within *Cladophora*, mussel clusters, or *Semibalanus* was significantly lower than for hatchlings on open surface plates (Fig. IV-5; ANOVA, $F=377.3$, $p<0.0001$, $n=12$). None of the hatchlings on open surface plates survived the four hours. Only 1.7% of hatchlings in *Cladophora* died, while average mortality for the other two microhabitats was ≈30 % (Fig. IV-5). Tufts of *C. columbiana* retain water when emersed; throughout four seasons of field work (1990-1993), naturally occurring

Figure IV-4. Size distribution of small *Nucella emarginata* in structurally complex microhabitats: the filamentous algae *Cladophora columbiana*, mussel clusters (*Mytilus californianus* and *M. trossulus*), and assemblages of large barnacles, *Semibalanus cariosus*. Pooled data from Wizard 1991 and 1992 and Ross 1992. Results are reported as a percentage of the total number of small snails in the same microhabitat. For example, 73% of snails ≤6 mm found in *Cladophora* were in the ≤1.5 mm size class, and 1.2% of *Cladophora* snails were in the 5.6 - 6.0 mm size class.

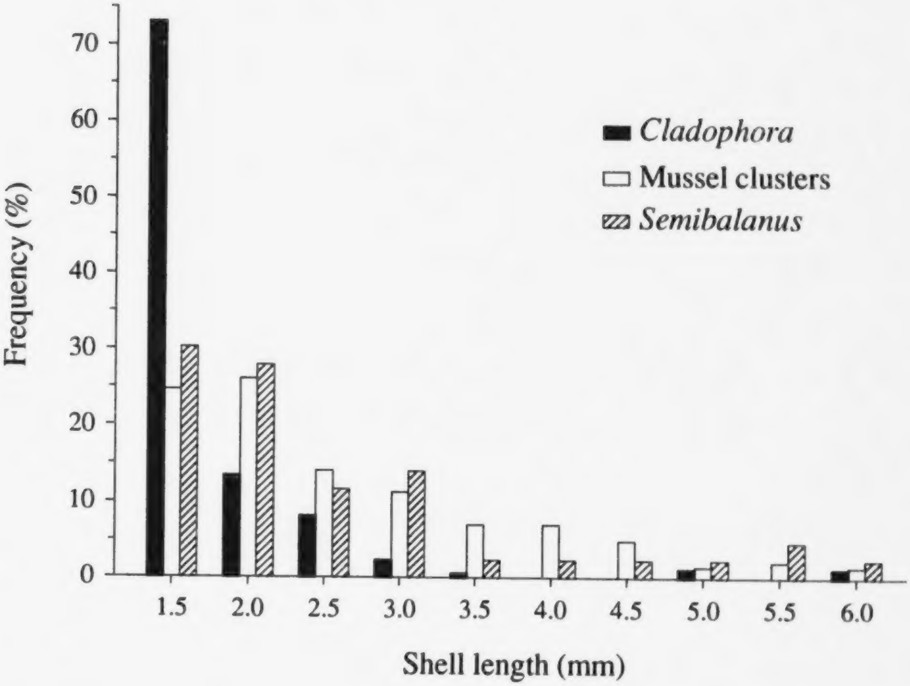
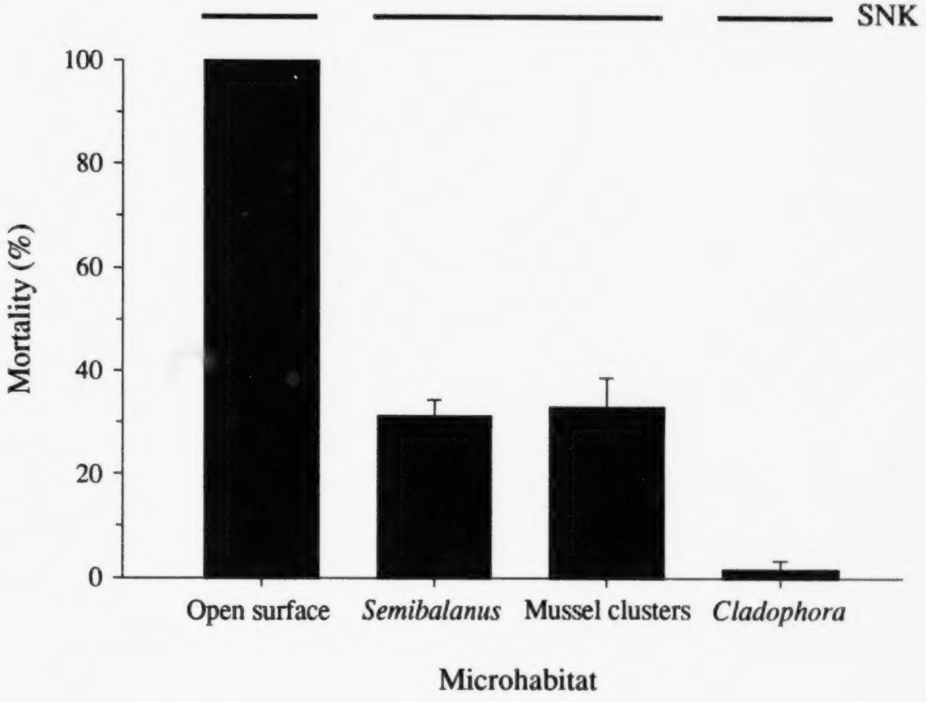

Frequency (%)
70
60
50
40
30
20
10
0
Cladophora
Mussel clusters
Semibalanus
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
6.0
Shell length (mm)

Figure IV-5. Mortality of newly hatched *Nucella emarginata* in four microhabitats exposed to desiccation. The microhabitat plates were placed in the intertidal zone at Wizard Islet for four hours on 11 September 1993. Lines above the graph indicate values that are not significantly different (Student-Neuman-Keuls grouping at $\alpha = 0.05$, $n = 3$ replicates of 20 hatchlings for each microhabitat). Error bars indicate standard errors.


SNK
Mortality (%)
100
80
60
40
20
0
Open surface
Semibalanus
Mussel clusters
Cladophora
Microhabitat

Cladophora were never observed to dry out at low tide, even when desiccating conditions were intense.

2.2 Protection from predators

Mortality of *Nucella emarginata* hatchlings exposed to three decapod predators for five hours in the laboratory was also considerably lower in *Cladophora*, mussel clusters, and among *Semibalanus* than on open surfaces (Fig. IV-6; ANOVA, F=73.8, $p<0.0001$, n=24). Hatchlings in the open surface treatment suffered 99.2% mortality, while in *Cladophora* and mussel microhabitats mortality was less than 16%.

3. Distribution of prey

Total prey densities were highest in *Cladophora* and barnacle microhabitats (Table IV-1, pooled results from both sites), with densities of up to 3105 prey / 100 cm^2. Small *Mytilus* and *Lasaea* were by far the most abundant prey at the time of sampling.

Prey species composition differed significantly between microhabitats both at Dixon Island (G = 3147.49, $p < 0.0001$, df = 15, R x C test of independence) and at Wizard Islet (G = 2675.76, $p < 0.0001$, df = 15), based on average prey densities in each microhabitat (Table IV-1). *Cladophora* only contained bivalves, open rock surfaces mainly supported small barnacles, and mussel clusters and *Semibalanus* contained specimens of all prey species (Table IV-1).

4. Dispersal of hatchlings

4.1 Dispersal in the water column

No hatchlings were caught in the *Cladophora* or in the mussel pouches of the collector on the three occasions when the collector was installed in the field. Water motion in the surge channel was nevertheless sufficient to suspend and transport small molluscs, as 100 - 300 juvenile *Mytilus* spp. (shell length ≤ 3 mm) recruited to the two microhabitats on each occasion. This also indicated that the contents of the pouches probably did simulate naturally occurring microhabitats reasonably well.

TABLE IV-1

Densities of species used as prey by *Nucella emarginata* hatchlings. Five samples (5 x 5 cm quadrats) of each microhabitat were collected at Dixon Island and at Wizard Islet in August 1993. Densities are given as average number / 100 cm^2 ± STD.

Prey species	Site	Microhabitats				ANOVA[3]
		Cladophora	*Semibalanus*[1]	Mussels[2]	Rock Surface	
Balanus glandula	Dixon	0.0	115.2±228.9	16.0±12.3	85.6±136.8	
	Wizard	0.0	30.4±16.6	11.2±12.5	112.8±172.0	F=1.85
	AVG	0.0	72.8±159.4	13.6±12.0	99.2±147.2	p=0.155
Chthamalus dalli	Dixon	0.0	36.0±65.5	0.8±1.8	148.8±116.6	
	Wizard	0.0	23.2±14.3	10.4±23.3	133.6±235.6	F=5.12
	AVG	0.0	29.6±45.3	5.6±16.4	141.2±175.4	p=0.005
		B	B	B	A	←SNK grouping
Mytilus spp. 0.5 - 5mm	Dixon	2056.0±508.7	548.0±428.3	609.6±195.6	1.6±2.2	
	Wizard	1108.0±482.8	254.4±107.2	152.8±81.1	2.4±3.6	F=40.0
	AVG	1582.0±684.3	401.2±332.5	381.2±279.1	2.0±2.8	p<0.0001
		A	B	B	C	←SNK grouping
Mytilus spp. 5 - 10mm	Dixon	9.6±6.1	16.0±4.0	72.0±43.2	0.0	
	Wizard	8.0±7.5	19.2±18.6	33.6±7.3	0.0	F=15.2
	AVG	8.8±6.5	17.6±12.8	52.8±35.5	0.0	p<0.0001
		B	B	A	B	←SNK grouping
Lasaea spp.	Dixon	1040.0±1099.1	1957.6±627.6	510.4±613.7	0.8±1.8	
	Wizard	116.0±43.5	508.8±166.3	509.6±361.1	0.8±1.8	F=7.21
	AVG	578.0±880.3	1233.3±877.7	510.0±474.7	0.8±1.7	p=0.0007
		B	A	B	B	←SNK grouping
Musculus taylori	Dixon	0.0	0.0	0.0	0.0	F=1.31
	Wizard	47.2±83.6	16.0±20.4	0.8±1.8	0.0	p=0.30[4]
Total prey	Dixon	3105.6±1572.6	2672.8±900.1	1208.8±511.0	236.8±194.1	
	Wizard	1279.2±439.8	852.0±223.1	718.4±363.2	249.6±397.8	F=11.3
	AVG	2192.4±1453.2	1762.4±141.5	963.6±491.4	243.2±295.2	p<0.0001
		A	A	B	B	←SNK grouping

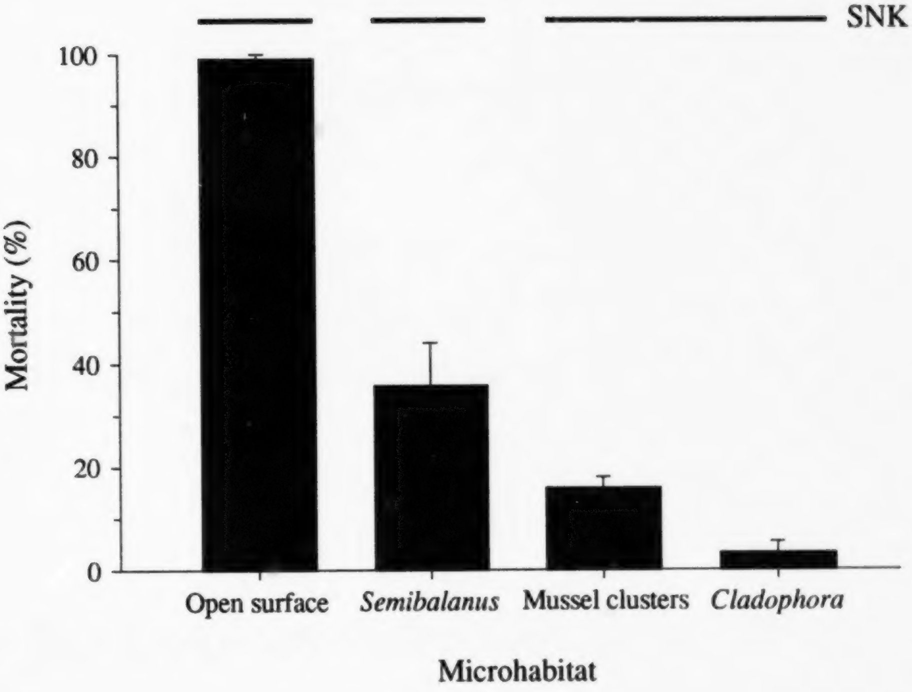
[1] Barnacle microhabitats consisted of assemblages of large *Semibalanus cariosus*.

[2] Mussel microhabitats consisted of clusters of *Mytilus californianus* and *M. trossulus*.

[3] Random complete block ANOVA using site as blocking factor, and Student-Neuman-Keuls grouping at $\alpha = 0.05$.

[4] Because no *Musculus* were found at Dixon Island, a one factor ANOVA was carried out on results from Wizard samples only.

Figure IV-6. Mortality of *Nucella emarginata* hatchlings in four microhabitats after five hours of exposure to two hermit crabs (one *Pagurus hirsutiusculus* and one *P. granosimanus*) and one shore crab (*Hemigrapsus nudus*). Lines above the graph indicate values that are not significantly different (Student-Neuman-Keuls grouping at $\alpha = 0.05$, $n = 6$ replicates of 20 hatchlings for each microhabitat). Error bars indicate standard errors.


SNK
Mortality (%)
100
80
60
40
20
0
Open surface
Semibalanus
Mussel clusters
Cladophora
Microhabitat

4.2 Crawling speed

Thirty-four hatchlings emerged from four capsules during the crawling speed experiments. These capsules had been collected from separate clutches in the field. The average crawling speed during the first 30 minutes after leaving the egg capsule was 3.70 ± 0.60 mm / minute (± STD), and ranged from 2.29 to 5.08 mm / minute.

Discussion

1. Distribution in the field

The distribution of recently hatched *Nucella emarginata* contrasted sharply with that of adults. Virtually all hatchlings were hidden in structurally complex microhabitats, while adults often appeared conspicuously on open surfaces. A more subtle shift was also apparent in *Cladophora* tufts; this filamentous alga appears to be the only microhabitat that is used only during a relatively brief period after hatching (Fig. IV-4). *Cladophora* retains a stiff, bush-like structure due to the turgor and slight calcification of the cells. As the snails grow, it is likely that this dense network increasingly hinders their movements until it is necessary to move to a different microhabitat. A more detailed analysis of the ontogenetic shift in microhabitat use by *N. emarginata* is presented in chapter VI.

The above pattern of microhabitat use by *N. emarginata* in Barkley Sound is probably of broader occurrence. For instance, Spight (1975) rarely found *N. emarginata* or *N. canaliculata* <5 mm shell length during almost six years of field work at several sites in Puget Sound, Washington, although snails >5 mm were found each year. Given the results of the present study, it may be that his observations were mostly limited to open surfaces. Also, after monthly collections of *N. lapillus* over a period of 17 months in Yorkshire, England, Feare (1970) reported that recently hatched individuals avoided open surfaces. The association of early juveniles with structurally complex microhabitats may therefore be a common feature of *Nucella* on temperate rocky shores.

Associations of small motile animals with structural refugia in benthic marine habitats can result from active microhabitat selection (Leber, 1985; Herrnkind and Butler, 1986; Main, 1987; Boudreau, 1990), differential mortality (Summerson and Peterson, 1984; Witman, 1985; Aronson, 1989), or possibly even dislodgement and relocation of individuals on open surfaces by waves and currents (Kohn and Leviten, 1976). The proximate cause of the distribution of early juvenile *N. emarginata* is not known. However, if hatchlings randomly moved between shelters and open surfaces, it is likely that they would rapidly be eliminated. Hence, behaviours favouring the use of structural refugia appear likely.

2. Significance of microhabitat use

Motile early juveniles of many benthic marine invertebrates are associated with structural refugia that are used only during a discrete period early in life, including lobsters (Barshaw and Lavalli, 1988; Wahle and Steneck, 1991; Smith and Herrnkind, 1992), mussels (Bayne, 1964; Petersen, 1984), nudibranchs (Sarver, 1979), scallops (Pohle et al., 1991), and snails (Underwood, 1976; Martel and Chia, 1991c; this study). Differential predation is often implicated as the ultimate cause of this association (Wilson et al., 1987; Martel and Chia, 1991c; Pohle et al., 1991; Wahle and Steneck, 1992; Smith and Herrnkind, 1992). The present study indicates that in the rocky intertidal zone, both predation and desiccation may act during alternate periods of the tidal cycle to cause substantially higher mortality of early juvenile snails that are not located in structural refugia.

Mortality of hatchling *N. emarginata* was indeed lower in structurally complex microhabitats than on open surfaces. More significant, however, was the magnitude of the difference in mortality over the short duration of the experiments: 99 - 100% of hatchlings on open surfaces died when exposed to desiccation or to predators for only four to five hours, while mortality of those in *Cladophora*, mussel clusters, or among *Semibalanus* was only 1.7 - 36%. Given the high predator densities at most field sites, reaching in excess of 400 ind. / m^2 (chapter III), and the daily exposure of intertidal habitats to desiccation at low tide, it is therefore probable that complex microhabitats are essential for the survival of hatchling *N. emarginata*. Individuals that fail to reach these shelters soon after hatching, or leave the shelters while still very small, incur a high risk of being killed within the following hours.

The microhabitats used by early juvenile *N. emarginata* provide the double advantage of low mortality risk and abundant prey, as *Cladophora*, mussel clusters and *Semibalanus* supported higher prey densities than open rock surfaces. Prey species content also differed between microhabitats, but this did not correspond to differences in prey value because *B. glandula* and *C. dalli* (mostly found on open surfaces) and *Mytilus* spp. (most abundant in *Cladophora*, mussel clusters, and among *Semibalanus*) are ranked similarly as the most favourable prey, based on growth rates of hatchlings feeding on single prey species (chapter V). Thus, prey in complex microhabitats were more abundant but of similar value to those on open rock surfaces.

The advantages provided by *Cladophora* (best protection against desiccation and predation, and highest density of prey) suggest this may be the most favourable microhabitat for newly hatched *N. emarginata*. However, the distribution of microhabitats in the field is patchy; given the limited motility of hatchling *N. emarginata*, *Cladophora* may not always be within reach or may not be encountered by certain hatchlings. Many *N. emarginata* would therefore remain in mussel clusters or among large *Semibalanus*; although these are less favorable microhabitats than *Cladophora*, they nevertheless provide substantial protection and abundant prey.

Previous studies have shown that structural complexity does not always provide an effective refuge against predators (Gosselin and Bourget, 1989), and may even enhance predation effects (Marinelli and Coull, 1987). In this study, complex microhabitats did protect hatchlings from predators. These same microhabitats, however, also contained high densities of species that are preyed upon by hatchlings. The effectiveness of a microhabitat as shelter from predators may therefore depend on the size ratio between predator and prey. Structural complexity can be an effective source of refuge from predators that are much larger than the prey, as is the case for crabs and hermit crabs that feed on small snails. However, when predators are of similar size or smaller than their prey, as is often the case for drilling gastropods, complex habitats are not likely to prevent access to the prey. In fact, such habitats may even provide the predator substantial protection from its own mortality factors, as is the case with early juvenile *N. emarginata* (this study) and adult *N. lapillus* (Gosselin and Bourget, 1989).

Werner and Gilliam (1984) suggested that small juvenile aquatic organisms should use habitats that minimize the ratio between mortality (μ) and growth (g) (i.e. minimize μ/g). For all sizes of *N. emarginata* the scope for growth will undoubtedly vary between microhabitats. In newly hatched individuals, however, differences in growth potential may be minimal relative to the differences in likelihood of being killed. Growth may therefore contribute little to differences in the μ/g ratio between habitats. If this is the case, patterns of habitat use would essentially be driven by μ until the organism reaches a size at which vulnerability has considerably decreased. Indeed, most newly hatched *N. emarginata* will not feed during the first days after emerging from their egg capsule even though feeding is essential to grow (chapter II), and it has been suggested that this allows them to find protection while living off reserves remaining from the egg capsule (chapter II). This indicates that the immediate need to avoid exposure to mortality factors may completely override activities necessary for growth.

3. Dispersal of hatchlings

During laboratory observations, undisturbed newly hatched *Nucella emarginata* did not raise a section of their foot, release mucous threads, or willingly detach from the substratum in response to turbulence or water flow, responses observed in gastropod species that actively disperse in the water column (Martel and Chia, 1991b). When dislodged, however, *N. emarginata* hatchlings are capable of producing mucus threads which effectively reduce sinking rates (Martel and Chia, 1991a; pers. obs.): this is undoubtedly an emergency measure used when they are dislodged by waves, macroalgae, or debris and carried into the water column. Mucus threads, up to 160 times the shell length (*Lacuna vincta*, Martel and Chia, 1991b), constitute an effective means of gaining contact with algae, rock, or shells, thereby increasing a dislodged hatchling's chances of reattaching onto a nearby structure before being carried away (Martel and Chia, 1991b).

The two *N. emarginata* hatchlings caught in off-bottom collectors by Martel and Chia (1991a) at an exposed site in Barkley Sound indicate that dispersal in the water column does occur, although it is probably infrequent. Dispersal in the water column is unlikely at protected sites because surface conditions are usually at their calmest (pers. obs.) during the period when most *N. emarginata* hatch (June to September, appendix 2), but may occur at sites exposed to intense wave action.

Crawling is therefore the usual means of travelling from the capsule to protective microhabitats. Hatchling crawling speed on a relatively smooth surface in the laboratory was only ≈22 cm / hour. Linear dispersal in the field is undoubtedly slower as a result of obstacles and surface irregularities.

On an ecological time scale, dispersal is therefore restricted to relatively short distances. Most individuals may indeed spend their entire life within a radius of a few meters of the position of the egg capsule from which they hatched (also see Palmer, 1984), and will be dependent on the resources and environmental conditions existing within that small area. On an evolutionary time scale, however, dispersal may be much greater that is currently assumed. Exchange of drifting hatchlings between adjacent groups of snails believed to be distinct populations may be sufficient to cause substantial gene flow. Since the prevalence of dislodgement and dispersal in the water column is likely to be proportional to wave-exposure, the geographic ranges of *N. emarginata* populations may correspondingly expand over increasing gradients of wave-exposure.

4. Conclusion

The use of protective microhabitats may be the key to survival through the vulnerable early juvenile period. Given that hatchlings can not survive the duration of a low tide when directly exposed to desiccation (chapter III; this study), it is essential that they reach a moisture-retaining microhabitat before they are exposed by the receding tide. In addition, hatchlings seeking shelter are exposed to decapod predators, which may even be waiting for them as they emerge from the egg capsules (chapter III).

The availability of microhabitats that protect early juveniles may be important in determining whether *N. emarginata* can colonize a given site, and set the upper limit of population abundance. As the three microhabitats occupied by hatchlings in the field consisted of sessile organisms, two of which can also be used as prey (*Mytilus* spp. and *Semibalanus cariosus*), populations of *N. emarginata* will therefore be indirectly dependant on factors that affect the abundance and distribution of these sessile organisms (also see Leviten and Kohn, 1980). Since the dispersal capabilities of small *N. emarginata* are limited, the distribution of protective microhabitats (e.g. many small patches vs. a few large patches) may be as important as their abundance in determining the size and distribution of *N. emarginata* populations.

In *N. emarginata*, individuals begin independent life at locations chosen by the female parent. Further study to determine whether females select spawning sites based on the proximity of microhabitats required by their offspring might therefore indicate a behavioural component of parental contribution in *N. emarginata*. Additional work is also needed to determine whether the distribution of early juvenile *N. emarginata* is a result of active microhabitat selection and, if so, to identify the cues used to locate and subsequently remain within protective microhabitats, as these will provide an understanding of the adaptations necessary to survive through the vulnerable early juvenile period.

References

Aronson, R.B. 1989. Brittlestar beds: low-predation anachronisms in the British Isles. Ecology. 70: 856-865.

Barshaw, D.E. and K.I. Lavalli. 1988. Predation upon postlarval lobsters, *Homarus americanus*, by cunners, *Tautogolabrus adspersus*, and mud crabs, *Neopanope sayi*, on three different substrates: eelgrass, mud, and rocks. Mar. Ecol. Prog. Ser. 48: 119-123.

Bayne, B.L. 1964. Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). J. Anim. Ecol. 33: 513-523.

Booth, J.D. 1979. Common bivalve larvae from New-Zealand: Leptonacea. N.Z. J. Mar. Freshwat. Res. 13: 241-254.

Boudreau, B., E. Bourget, and Y. Simard. 1990. Benthic invertebrate larval response to substrate characteristics at settlement: shelter preferences of the American lobster *Homarus americanus*. Mar. Biol. 106: 191-198.

Crothers, J.H. 1985. Dogwhelks: an introduction to the biology of *Nucella lapillus* (L.). Field Studies. 6: 291-360.

Feare, C.J. 1970. Aspects of the ecology of an exposed shore population of dogwhelks *Nucella lapillus* (L.). Oecologia 5: 1-18.

Gosselin, L.A. and E. Bourget. 1989. The performance of an intertidal predator *Thais lapillus*, in relation to structural heterogeneity. J. Anim. Ecol. 58: 287-303.

Gosselin, L.A. and P.-Y. Qian. Submitted. Early postsettlement mortality of an intertidal barnacle: a critical period for survival. Ecology.

Herrnkind, W.F. and M.J. Butler, IV. 1986. Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobsters, *Panulirus argus*. Mar. Ecol. Prog. Ser. 34: 23-30.

Kohn, A.J. and P.J. Leviten. 1976. Effect of habitat complexity on population density and species richness in tropical intertidal predatory gastropod assemblages. Oecologia. 25: 199-210.

Leber, K.M. 1985. The influence of predatory decapods, refuge, and microhabitat selection on seagrass communities. Ecology. 66: 1951-1964.

Leviten, P.J. and A.J. Kohn. 1980. Microhabitat resource use, activity patterns, and episodic catastrophe: *Conus* on tropical intertidal reef rock benches. Ecol. Monogr. 50: 55-75.

Main, K.L. 1987. Predator avoidance in seagrass meadows : prey behavior, microhabitat selection, and cryptic coloration. Ecology. 68: 170-180.

Marinelli, R.L. and B.C. Coull. 1987. Structural complexity and juvenile fish predation on meiobenthos: an experimental approach. J. Exp. Mar. Biol. Ecol. 108: 67-81.

Martel, A. and F.-S. Chia. 1991a. Drifting and dispersal of small bivalves and gastropods with direct development. J. Exp. Mar. Biol. Ecol. 150: 131-147.

Martel, A. and F.-S. Chia. 1991b. Foot-raising behaviour and active participation during the initial phase of post-metamorphic drifting in the gastropod *Lacuna* spp.. Mar. Ecol. Prog. Ser. 72: 247-254.

Martel, A. and F.-S. Chia. 1991c. Oviposition, larval abundance, in situ larval growth and recruitment of the herbivorous gastropod *Lacuna vincta* in kelp canopies in Barkley Sound, Vancouver Island (British Columbia). Mar. Biol. 110: 237-247.

Mittelbach, G.G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). Ecology. 65: 499-513.

Moore, H.B. 1938. The biology of *Purpura lapillus*. Part III. Life history and relation to environmental factors. J. Mar. Biol. Ass. UK. 23: 67-74.

Palmer, A.R. 1984. Species cohesiveness and genetic control of shell colour and form in *Thais emarginata* (Prosobranchia, Muricacea); preliminary results. Malacologia 25: 477-491.

Palmer, A.R. 1985. Genetic basis of shell variation in *Thais emarginata* (Prosobranchia, Muricacea). I. Banding in populations from Vancouver Island. Biol. Bull. 169: 638-651.

Palmer, A.R. 1990. Predator size, prey size, and the scaling of vulnerability: hatchling gastropods vs. barnacles. Ecology. 71: 759-775.

Palmer, A.R., S.D. Gayron, and D.S. Woodruff. 1990. Reproductive, morphological, and genetic evidence for two cryptic species of Northeastern Pacific *Nucella*. Veliger. 33: 325-338.

Petersen, J.H. 1984. Larval settlement behavior in competing species: *Mytilus californianus* Conrad and *M. edulis* L.. J. Exp. Mar. Biol. Ecol. 82: 147-159.

Pohle, D.G., V.M. Bricelj, and Z. Garcia-Esquivel. 1991. The eelgrass canopy: an - above-bottom refuge from benthic predators for juvenile bay scallops *Argopecten: irradians*. Mar. Ecol. Prog. Ser. 74: 47-59.

Sarver, D.J. 1979. Recruitment and juvenile survival in the sea hare *Aplysia juliana* (Gastropoda: Opisthobranchia). Mar. Biol. 54: 353-361.

Sellmer, G.P. 1967. Functional morphology and ecological life history of the gem clam, *Gemma gemma* (Eulamellibranchia: Veneridae). Malacologia. 5: 137-223.

Smith, K.N. and W.F. Herrnkind. 1992. Predation on early juvenile spiny lobsters *Panulirus argus* (Latreille): influence of size and shelter. J. Exp. Mar. Biol. Ecol. 157: 3-18.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. W.H. Freeman and Co., New York, NY, Second edition. 859 pp.

Sorlin, T. 1988. Floating behaviour in the tellinid bivalve *Macoma balthica* (L.). Oecologia. 77: 273-277.

Spight, T.N. 1974. Sizes of populations of a marine snail. Ecology. 55: 712-729.

Spight, T.M. 1975. On a snail's chances of becoming a year old. Oikos. 26: 9-14.

Spight, T.M. 1982. Population sizes of two marine snails with a changing food supply. J. Exp. Mar. Biol. Ecol. 57: 195-217.

Summerson, H.C. and C.H. Peterson. 1984. Role of predation in organizing benthic communities of a temperate-zone seagrass bed. Mar. Ecol. Prog. Ser. 15: 63-77.

Thorson, G. 1966. Some factors influencing the recruitment and establishment of marine benthic communities. Neth. J. Sea Res. 3: 267-293.

Underwood, A.J. 1976. Analysis of patterns of dispersion of intertidal prosobranch gastropods in relation to macroalgae and rock-pools. Oecologia. 25: 145-154.

Underwood, A.J. 1979. The ecology of intertidal gastropods. Adv. Mar. Biol. 16: 111-210.

Vermeij, G.J. 1972. Intraspecific shore-level size gradients in intertidal molluscs. Ecology. 53: 693-700.

Vermeij, G.J. 1978. Biogeography and Adaptation. Patterns of Marine Life. Harvard University Press, Cambridge, Massachussetts, USA. 332 p.

Vermeij, G.J. 1987. Evolution and Escalation. An Ecological History of Life. Princeton University Press, Princeton, New Jersey, USA. 527 p.

Wahle, R.A. and R.S. Steneck. 1991. Recruitment habitats and nursery grounds of the American lobster *Homarus americanus*: a demographic bottleneck? Mar. Ecol. Prog. Ser. 69: 231-243.

Wahle, R.A. and R.S. Steneck. 1992. Habitat restrictions in early benthic life: experiments on habitat selection and in situ predation with the American lobster. J. Exp. Mar. Biol. Ecol. 157: 91-114.

Werner, E.E. and J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst. 15: 393-425.

Werner, E.E., J.F. Gilliam, D.J. Hall, and G.G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology. 64: 1549-1555.

Werner, E.E. and D.J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology. 69: 1352-1366.

Wilson, K.A., K.W. Able, and K.L. Heck, Jr.. 1987. Juvenile blue crab, *Callinectes sapidus*, survival: an evaluation of eelgrass, *Zostera marina*, as refuge. Fish. Bull. 85: 53-58.

Witman, J.D. 1985. Refuges, biological disturbance, and rocky subtidal community structure in New England. Ecol. Monogr. 55: 421-445.

CHAPTER V

Prey species and prey size selection by inexperienced predators: prey preferences of newly hatched intertidal snails.

Introduction

Foraging experience can be an important basis for decisions that influence searching and handling efficiency as well as food preferences (Wood, 1968; Hughes, 1979; Derby and Atema, 1981; Bayliss, 1982; Johnson, 1991). Through a series of encounters with prey, individuals may learn to become more efficient at locating prey, feed on fewer species or on a narrower range of sizes of prey, and abandon less efficient methods of attack (Hughes, 1980; Hughes and Dunkin, 1984a; Johnson, 1991). It is not known, however, if organisms that make foraging decisions based on experience require this experience to be selective.

The advantages of using intertidal snails for studying foraging behaviour are well documented (Palmer, 1984, 1990; Hughes and Burrows, 1991). *Nucella emarginata* (Deshayes) (northern, cf. Palmer et al., 1990), an intertidal predatory gastropod, is particularly suitable for studying the selectivity of experienced and inexperienced individuals. Prior feeding experience influences decisions regarding selection of prey species and size in late juvenile and adult *N. emarginata* (Palmer, 1984) and other thaidine gastropods (Menge, 1974; Palmer, 1984; Hughes and Dunkin, 1984b). However, when *N. emarginata* hatch, after having completed larval development within a benthic egg capsule, they have no direct information on the distribution, abundance, or value of nearby prey. Newly hatched muricids may obtain some information through chemosensory detection of prey (Williams et al., 1983), although the usefulness of this information is unclear. Chemotactic responses to prey species may in fact be suppressed by exposure to their odours during development (Rittschof et al., 1984). In any case, prey odours would not provide detailed knowledge of the abundance and distribution of nearby prey. In addition, snails emerging from their egg capsule have no experience pertaining to the costs and benefits of each prey type.

When newly hatched *N. emarginata* search for food items for the first time they must decide whether to attack or reject each item encountered without the benefit of experience from previous encounters. As a result, young snails might be expected to be less selective than older individuals. Yet, selective foraging during the early juvenile period could provide substantial benefits. Newly hatched *N. emarginata* are extremely vulnerable to predators and physical stresses (chapter III) and cohorts of intertidal thaidine gastropods suffer considerable mortality early in life (Feare, 1970; Spight, 1975). Selecting prey that promote the fastest growth could be beneficial to hatchlings because this might shorten the period during which they were in the smallest, most vulnerable sizes (Vermeij, 1972, 1978, 1987; Werner and Gilliam, 1984; chapters III and VI). In addition, Gosselin (chapter IV) found that the distribution of two bivalve species used as prey by hatchling *N. emarginata* (*Lasaea* spp. and *Mytilus* spp.) were similar to that of hatchlings and consequently suggested that these prey species might be used as cues to locate and then remain within protective microhabitats. For this animal, strong prey preferences established at the onset of independent benthic life might enhance survival through the early juvenile period if they prefer prey that are mainly located in microhabitats providing substantial protection from mortality factors.

The objectives of this study were therefore to: 1) examine prey species and prey size selection by newly hatched *N. emarginata* when attacking their first prey to determine if inexperienced hatchlings are less selective than older, experienced individuals, and thus if feeding experience is the main basis for selective foraging; 2) determine if hatchlings select prey that promote the fastest growth, consistent with the energy maximization hypothesis of optimal foraging theory (Pyke et al., 1977; Hughes, 1980; Palmer, 1983); and 3) compare prey preferences (this study) with the distribution of prey in the field (chapter IV) to determine if newly hatched *N. emarginata* prefer prey that are located in microhabitats providing the best protection, and examine the potential of prey preferences as a mechanism for locating protective microhabitats.

Materials and Methods

1. Study site and organism

The experiments described herein were carried out at the Bamfield Marine Station, British Columbia, Canada, from December 1991 to September 1992. All organisms were collected at nearby sites in Barkley Sound. Hatchlings used in the following experiments had been spawned in the field and had undergone complete larval development in their natural environment. Ripe capsules (unplugged capsules containing metamorphosed individuals that had not yet emerged) were collected and placed in cages in flowing seawater in the laboratory. Hatchlings that emerged in the laboratory during the first 24 hours after collecting the capsules were placed in a separate cage until later use; the age of the hatchlings used in each experiment could therefore be determined with an accuracy of 24 hours (time of emergence is considered t = 0). Because most *N. emarginata* do not feed during the first 3 - 10 days after emerging from their egg capsule (chapter II), newly hatched individuals (1.0 - 1.9 mm shell length) were placed in otherwise empty cages in flowing seawater for 15 to 18 days before being used in the following experiments. These hatchlings therefore had no contact with prey prior to experimentation. Each snail was used only once in this study.

2. Prey preferences

2.1 Prey species selection

To determine if prey species preferences are established before feeding experience is acquired, *Nucella emarginata* hatchlings from Kirby Point (48°50'85"N, 125°12'40"W) were enclosed with five prey species (*Mytilus* spp., *Lasaea* spp., *Balanus glandula*, *Chthamalus dalli*, and *Pollicipes polymerus*) and the first item to be attacked was identified. Of the six species that can be used as prey by newly hatched *N. emarginata* (chapter II) only *Musculus taylori* was not offered, as this species was absent or rare at most field sites (chapter IV) and could not be found in sufficient quantities at the time of this experiment. Very small cages (modified centrifuge micro test tubes, 11 mm diam. x 14 mm long, provided with 610 µm mesh screening), hereafter referred to as micro cages, received one hatchling and the following five prey items: one small *Mytilus* (2 - 3 mm shell length; includes *M. trossulus* and *M. californianus* which could not be distinguished at this size), one *Balanus* (2 - 4 mm shell diameter, rostro-carinal axis), one *Chthamalus* (2 - 4 mm shell diameter), one *Lasaea* (2 - 3 mm shell length), and one *Pollicipes* (2 - 3 mm shell diameter, measured at the widest area of the scutum). Individual *Balanus* and *Chthamalus* were obtained by breaking off small pieces of mussel and barnacle shells to which they were attached. *Pollicipes* were gently detached from the bases of adults and placed in flowing seawater for 48 hours; individuals surviving this period were used in the present experiment. The cages containing predators and prey then were placed in flowing seawater for 3.75 days, after which each prey item was examined under a dissecting microscope for evidence of drilling. All attacks, complete and incomplete, were recorded. In most cases hatchlings only had time to attack one prey.

2.2 Prey size selection

Based on the results of the prey species selection experiment, hatchlings obtained from Dixon Island (48°51'15"N, 125°06'90"W) were offered a range of sizes of small *Mytilus* spp., the preferred species, to determine if inexperienced hatchlings also had prey size preferences. One hatchling and five mussels, of 1 (1.04 - 1.25 mm), 2 (1.8 - 2.2 mm), 3 (2.8 - 3.2 mm), 4 (3.8 - 4.2 mm), and 5 mm (4.8 - 5.2 mm) shell length size classes, were placed in micro cages for five days. All mussels were then examined under a dissecting microscope for evidence that the shell had been drilled.

3. Significance of prey preferences

If foraging decisions made by inexperienced hatchlings are consistent with the energy maximization premise, prey that provide the greatest energy return should be preferred. To determine if this is the case, growth of hatchlings, prey energy content, and the time required to drill the prey were examined.

3.1 Hatchling growth vs. prey species

The net energetic benefit of each prey species to hatchlings was examined by providing hatchlings with a single prey species for 25 days and measuring their growth over this period. Hatchlings 16 - 19 days old were individually marked with nail polish colour codes using the method described in Appendix 1, and were measured using the ocular micrometer of a dissecting microscope (± 0.0392 mm). Marked hatchlings were then placed in cages (modified plastic vials, 39 mm diam. x 62 mm long, hereafter referred to as vial cages), three cages for each prey species, containing 6 or 7 hatchlings ($n = 20$ hatchlings per prey treatment). Hatchlings were offered either *Mytilus* spp. (1 - 10 mm shell length), *Balanus glandula* (2 - 8 mm shell diameter), *Chthamalus dalli* (1.5 - 6 mm shell diameter), *Lasaea* spp. (1.5 - 4.5 mm shell length), or *Pollicipes polymerus* (2 - 10 mm shell diameter). Each cage contained 70 - 120 prey items. To determine if a varied diet can produce faster growth, an additional set of three vial cages each containing 24 items of each prey species was also included in the experiment. The cages were then placed in three aerated 40 litre aquaria; each aquaria received one cage from each prey treatment. After 25 days all hatchlings were remeasured. Hatchlings did not consume more than 75% of the prey items during the 25 day period, so that prey availability was not believed to be a limiting factor.

3.2 Energy content of prey

To compare prey energy density between size classes and species, the volume and energy content of three size classes of *Mytilus* spp., *Lasaea* spp., *Chthamalus dalli*, and *Balanus glandula* were measured in September 1992. The body volume of individual prey items was determined using water displacement measurements. For the two barnacle species (*Balanus* and *Chthamalus*), individuals were obtained by gently detaching the base of their shell from the rock surface using the blade of a scalpel. If flesh remained attached to the rock, the individual was not used. These results were then used to calculate a regression equation between body volume and shell length (*Mytilus* and *Lasaea*) or diameter (*Chthamalus* and *Balanus*) (Table V-1). For *Mytilus* and *Lasaea*, these equations were then used to determine the ranges in shell length corresponding to the 1.0 - 1.9 µl, 2.0 - 2.9 µl, and 3.0 - 3.9 µl volume classes. For *Chthamalus* and *Balanus*, however, the correlation between diameter and body volume was not as strong

TABLE V-1

Relationship between body volume and linear size measurements of four species used as prey by *Nucella emarginata* hatchlings. Regression equations were calculated using 0 as intercept.

Prey species	Regression equation[*]	R^2	n	Size range measured	Collection site
Mytilus spp.	Vol=0.095xSL^3	0.974	24	1.52-5.92 mm SL	Wizard Islet
Lasaea spp.	Vol=0.175xSL^3	0.960	24	0.96-3.12 mm SL	Wizard Islet
Chthamalus dalli	Vol=0.056xSD^3	0.783	24	1.58-3.36 mm SD	Ross Islets
Balanus glandula	Vol=0.096xSD^3	0.919	23	2.56-7.6 mm SD	Ross Islets

[*] Vol: body volume (µl); SL: shell length (mm); SD: shell diameter, measured along rostro-carinal axis (mm).

(Table V-1); volume measurements were therefore carried out for each specimen included in the energy content analysis.

New samples of prey were then collected from the field, individuals of appropriate sizes were selected and, within 24 hours of collection, their energy content was determined by dichromate oxidation against a glucose standard using the method described by McEdward and Carson (1987). This method quantifies total organic carbon; organic carbon values were converted to total energy using the formula: 1 μg C = 3.90 x 10^{-2} J, based on constants in Parsons et al. (1984). Because the amount of organic material present in the smallest individuals was close to the limits of detection of the method, more than one individual were placed in each replicate test tube for the smallest size classes as follows: 1.0 - 1.9 μl, three individuals; 2.0 - 2.9 μl, two individuals; 3.0 - 3.9 μl, one individual. Volume and energy content measurements were then used to calculate energy density (J / μl body volume).

Some reduction in accuracy will have resulted from the use of total body volume rather than internal body cavity volume to calculate energy density. Also, the use of the entire animal, including the shell, in the dichromate oxidation analysis can affect the results. Although the shell contains relatively little organic material (<5 % by weight in mollusc shells, Lowenstam and Weiner, 1989), it becomes pulverised during the procedure and when suspended may interfere with spectrophotometer readings. I found, however, that the shell material sedimented out of the solution within 24 hours; readings from the glucose standards did not change over this period. Consequently, spectrophotometer readings were taken 24 hours after oxidation of the samples.

3.3 Time required to drill prey species

The time necessary for inexperienced *Nucella emarginata* hatchlings to drill through their prey was examined to determine if hatchlings prefer prey species which require the least handling time. Twenty 22-day old hatchlings were placed in each of 16 vial cages with small *Mytilus* spp. (1.5 - 3.5 mm shell length), *Balanus glandula* (1.6 - 5.6 mm shell diameter), *Chthamalus dalli* (1.4 - 5.0 mm shell diameter), or *Lasaea* spp. (1.2 - 3.0 mm shell length). Each vial cage received at least 40 individuals of one prey species. These cages were placed in flowing seawater and a set of four cages, one cage for each prey species, was recovered after each interval (12, 18, 24, and 48 hours). All prey individuals were then closely examined for evidence that they had been drilled. Drill holes that did not completely penetrate the prey's shell were recorded as incomplete attacks; drill holes that opened into the prey's body cavity were recorded as complete. The present measurements of drilling time, however, also include the time taken by the hatchling to find the prey and position itself on the prey's shell. Given the small size of the micro cages, the inclusion of three prey per cage, and the initial placement of hatchling and prey together at the bottom of each cage, it is probable that the time used to find the prey and select a position on its shell was short and depended mainly on the snail's willingness to attack the prey.

Results

1. Prey preferences

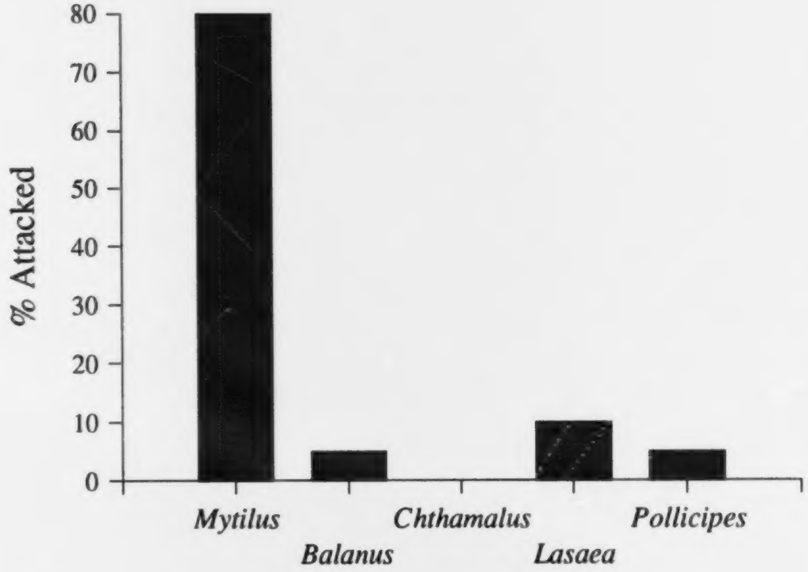
1.1 Prey species selection

When attacking their first prey, *Nucella emarginata* hatchlings did not attack randomly: observed attack frequencies were significantly different from expected frequencies based on an even distribution of attacks among species (single attacks, Goodness of fit test: $G_{adj} = 34.327$, $p < 0.001$, df = 4; G value adjusted using Williams' correction, Sokal and Rohlf, 1981). *Mytilus* spp. was attacked much more often that any other species (Fig. V-1). Of the 20 hatchlings attacking only one prey item, 80% attacked *Mytilus*. In each case where hatchlings had attacked two (n = 2) or three (n = 1) items, *Mytilus* was one of the attacked prey.

1.2 Prey size selection

If inexperienced hatchlings attacked *Mytilus* as they encountered them, the distribution of attacks among size classes should reflect some measurement of mussel body size, the likelihood of encounter increasing with size. An expected attack frequency was calculated, which assumed no size selection by the hatchlings, using mussel body volume as an indicator of the likelihood of encounter. Although a two-dimensional measurement of area occupied by the mussel might seem more appropriate, the actual area

Figure V-1. Prey species attacked by hatchling *Nucella emarginata* encountering prey for the first time. Twenty hatchlings were individually placed in micro cages with one item of each prey species for 3.75 days. Hatchlings did not attack more than one prey item in this experiment. Values shown are the percentage of attacks on each of five prey species. Attack frequencies were significantly different from a 1:1:1:1:1 ratio (see text).


% Attacked
0
10
20
30
40
50
60
70
80
Mytilus
Balanus
Chthamalus
Lasaea
Pollicipes

occupied would vary depending on the position of the mussel relative to the substratum. The volume occupied by a mussel, however, remains constant regardless of its position, and was therefore used as a simple, although less conservative, way of approximating relative likelihood of encounter. Mussel volume for each size class was calculated using the regression equation in Table V-1.

The expected and actual attack frequencies showed contrasting patterns (Fig. V-2). Of the 22 hatchlings that attacked a single mussel during the five day period, 72.7% of these attacked 1 or 2 mm prey (single attacks, Fig. V-2). Attacks on 4 and 5 mm mussels totalled only 9.1%. A similar pattern was obtained when results from the remaining 13 hatchlings that attacked two prey were included (all attacks, Fig. V-2). Single attack frequencies were significantly different from expected attack frequencies using body volume as an indicator of encounter likelihood (Goodness of fit test: $G_{adj} = 97.871$, $p < 0.001$, df = 4). Although 5 mm mussels occupied 125 times more space than 1 mm mussels, 1 mm mussels were attacked 8 times more often.

2. Significance of prey preferences

2.1 Hatchling growth vs. prey species

Hatchling growth differed significantly among prey species treatments (ANOVA: $F = 3.36$, $p = 0.013$, $n = 89$). Hatchlings feeding on *Lasaea* spp. grew less during the 25 day period than did hatchlings feeding on other species (Fig. V-3). However, no significant difference in growth was detected between hatchlings provided with *Mytilus* spp., *Balanus glandula*, *Chthamalus dalli*, or all five prey species.

No growth data were obtained from snails feeding on *Pollicipes polymerus*. Eighteen of the 20 hatchlings in this treatment died and the other two did not grow. Most of the large *Pollicipes* died and were in an advanced state of decomposition at the end of the 25 day period. Because this species is typically found at sites exposed to intense wave action or high currents, it presumably could not tolerate the comparatively low flow conditions existing in the cages. In each of the other prey treatments, a maximum of three out of 20 hatchlings died.

Figure V-2. *Mytilus* spp. sizes attacked by hatchling *Nucella emarginata* encountering prey for the first time. Thirty-five hatchlings were individually placed in micro cages with one mussel of each size class for five days. Values shown are the percentage of attacks on each of five size classes by hatchlings that attacked only one prey (single attacks, n = 20) or by hatchlings that attacked either one or two prey items (all attacks, n = 35). Also shown are the attack frequencies expected if mussels were attacked as they were encountered, using mussel body volume as an estimator of likelihood of encounter.

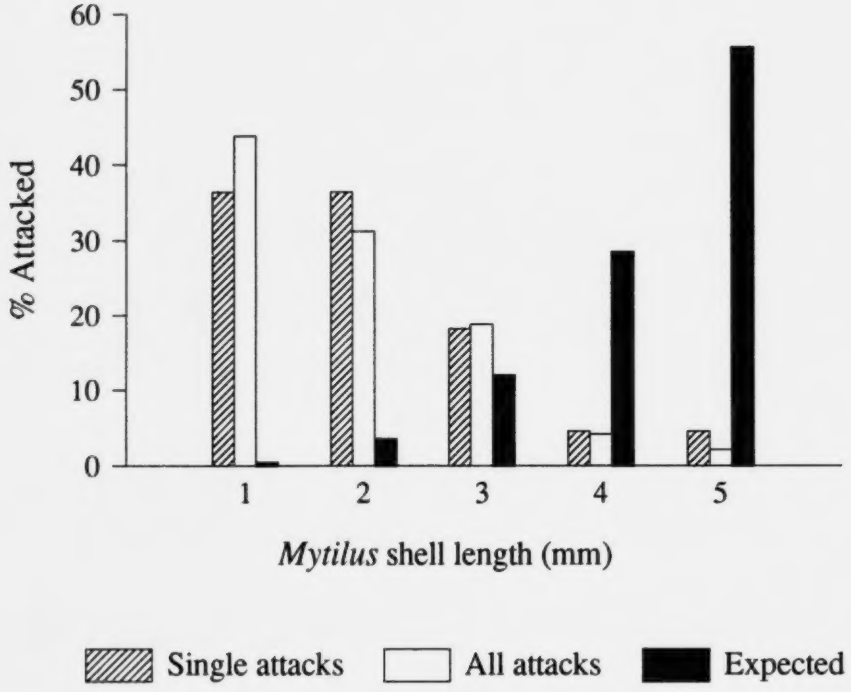
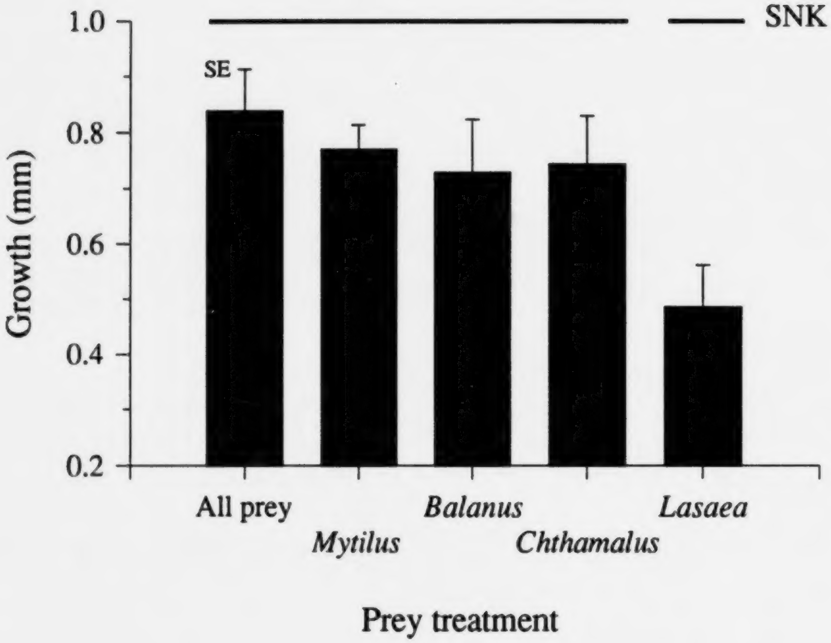

60
50
40
30
20
10
0
% Attacked
1
2
3
4
5
Mytilus shell length (mm)
Single attacks
All attacks
Expected

Figure V-3. Growth of *Nucella emarginata* hatchlings provided with five prey species (all prey treatment) or with single prey species over a period of 25 days. The lines along the top of the figure indicate mean values that were not significantly different (Student-Neuman-Keuls grouping, $\alpha = 0.05$, $n = 16$ to 19 per treatment).


1.0
0.8
0.6
0.4
0.2
Growth (mm)
SE
SNK
All prey
Mytilus
Balanus
Chthamalus
Lasaea
Prey treatment

2.2 Energy content of prey

Within each prey species the amount of energy per unit body volume (J / µl; Fig. V-4) did not differ significantly between size classes (ANOVA: *Mytilus* spp.: F = 0.21, p = 0.816, n = 21; *Chthamalus dalli*: F = 1.62, p = 0.226, n = 21; *Lasaea* spp.: F = 0.91, p = 0.358, n = 14). Data from different size classes were therefore pooled for between-species comparisons. Energy densities were significantly different between species (ANOVA, F = 4.88, p = 0.011), being higher in *Mytilus* and *Chthamalus* than in *Lasaea* (Fig. V-4). Energy density of *Mytilus* and *Chthamalus* were not significantly different. Inaccurate results were obtained when analyzing the energy content of *Balanus glandula* due to manipulation errors, and these results could not be used.

2.3 Time required to drill prey species

Hatchlings feeding on *Mytilus* spp. generally completed their drill hole sooner than those feeding on *Balanus glandula* or *Chthamalus dalli*. *Lasaea* were also drilled through rapidly, but few hatchlings bothered to attack *Lasaea* (Fig. V-5a). Incomplete attacks on mussels were rarely observed, and many hatchlings had finished drilling through *Mytilus* within the first 12 hours (Fig. V-5). In a preliminary experiment where 21-day old hatchlings were placed directly on small mussels (≤3 mm), the shortest time required to drill through the prey's shell was six to eight hours.

In the present study, several hatchlings attacked *Balanus* and *Chthamalus* during the first 12 hours (Fig. V-5a), but the drill holes were usually incomplete, and many attacks were still not complete after 48 hours (Fig. V-5b). In addition, some hatchlings abandoned incomplete attack sites on *Balanus* and started new attacks on other prey items or occasionally at a different site on the same prey item. Attack sites on *Chthamalus* were rarely abandoned prior to completion, and such unsuccessful attacks were not observed among hatchlings feeding on *Mytilus* or *Lasaea*.

Figure V-4. Energy density, in J / µl, of three size classes of *Mytilus* spp., *Chthamalus dalli*, and *Lasaea* spp. (n = 7 for each value shown). Few 3.0 - 3.9 µl *Lasaea* were obtained at the time of the study, and thus no results are available for *Lasaea* in this size class. Energy density of size classes of a same species were not significantly different (see text). The lines along the top of the figure indicate the overall species averages that were not significantly different (Student-Neuman-Keuls grouping, $\alpha=0.05$, n = 14 (*Lasaea*) or 21 per treatment).

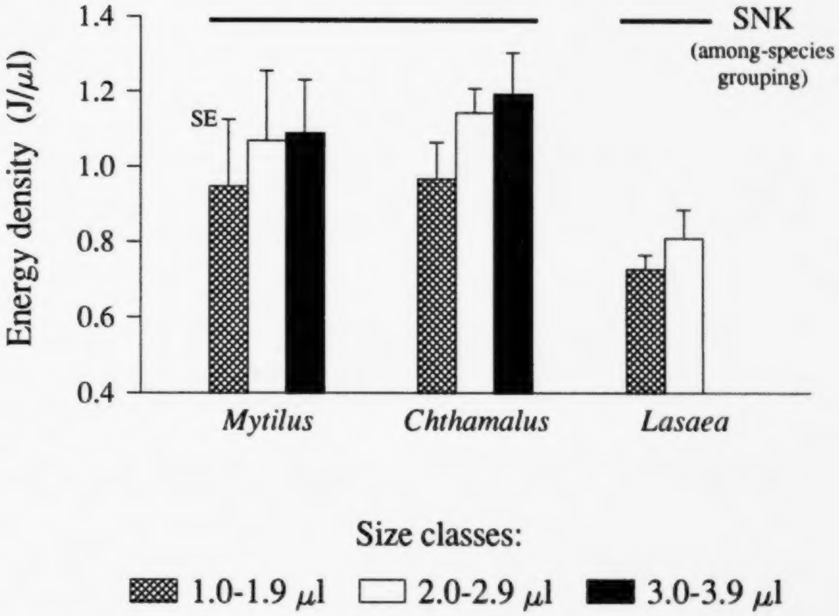
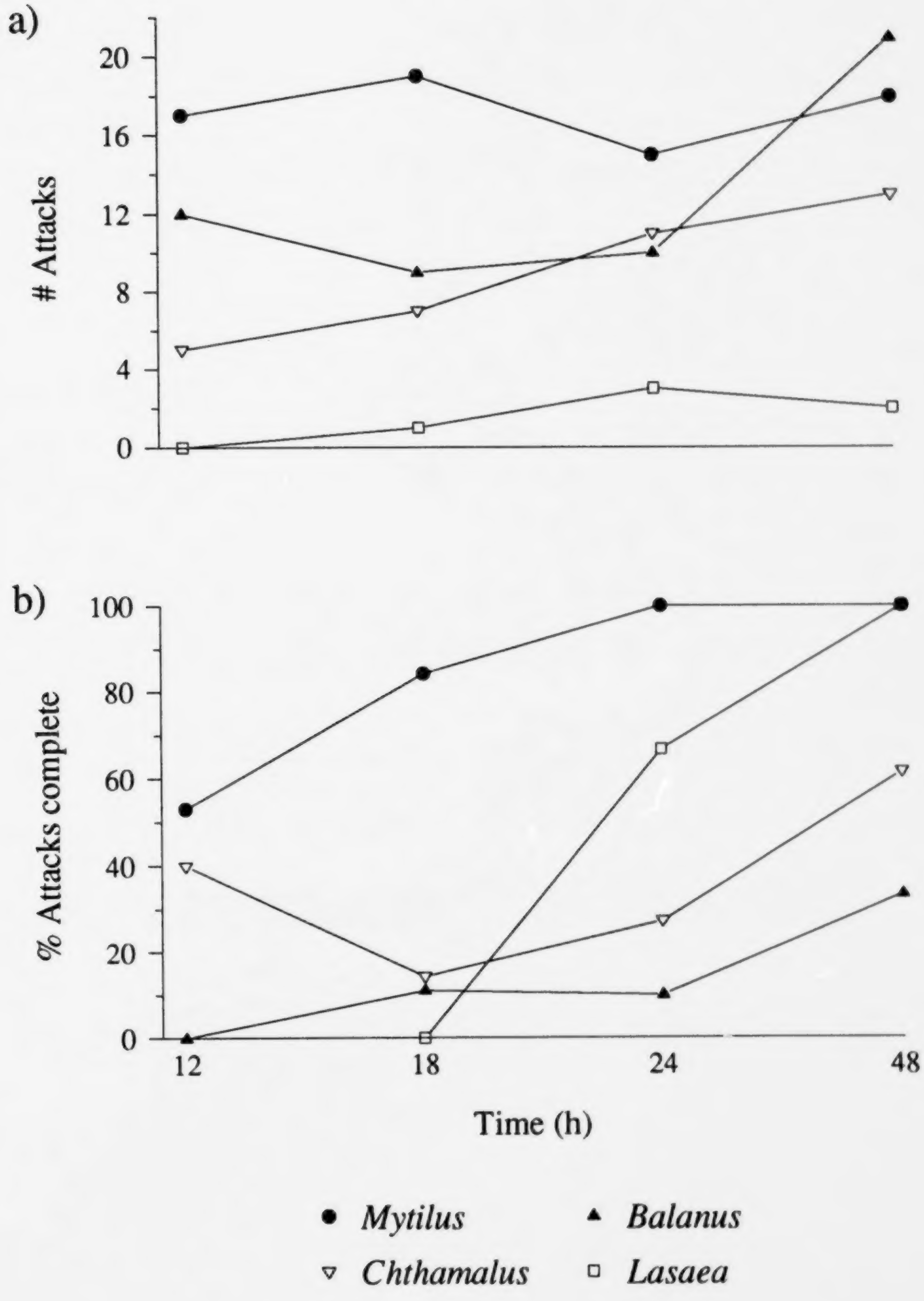

1.4
1.2
1.0
0.8
0.6
0.4
Energy density (J/μl)
SE
SNK
(among-species grouping)
Mytilus
Chthamalus
Lasaea
Size classes:
1.0-1.9 μl
2.0-2.9 μl
3.0-3.9 μl

Figure V-5. Time required by hatchling *Nucella emarginata* to drill through the shell of four species of prey. A new set of vial cages, one per prey species, was recovered after each time interval. Each cage contained 20 hatchlings and ≥40 prey items. a) Total number of attacks on each species. b) Percentage of attacks in which the drill hole was completed through to the body cavity of the prey.


a)
# Attacks
0
4
8
12
16
20
b)
% Attacks complete
0
20
40
60
80
100
12
18
24
48
Time (h)
● *Mytilus*
▲ *Balanus*
▽ *Chthamalus*
□ *Lasaea*

Discussion

1. Prey selection by inexperienced individuals

Hatchling *Nucella emarginata* can feed and grow on any of the species offered in this study (Fig. V-3), and they do feed at least occasionally on these species in the field (chapter II). In the laboratory, *N. emarginata* can be reared for several generations on a diet of barnacles (Palmer, 1985). When attacking their first prey item, however, hatchlings attacked *Mytilus* spp. considerably more often than any of the other four species offered. In addition, inexperienced hatchlings mainly attacked 1 - 2 mm mussels, the smallest available size classes. The high attack rates of newly hatched *N. emarginata* on very small *Mytilus* were the result of behavioral selection of prey species and size. For instance, even the largest *Mytilus* size class offered (5 mm shell length) was well within the range of sizes that hatchlings can successfully attack, since mussels as large as 10 mm have been successfully drilled through by hatchlings in the laboratory, and 5 mm mussels were readily consumed when these alone were offered as prey (pers. obs.). The strong preference for small *Mytilus* was repeatedly observed in different feeding experiments using hatchlings from other sites in Barkley Sound (chapter II; pers. obs.).

During the first four weeks after hatching, *N. lapillus* can feed on a variety of prey species (Largen, 1967), but small mussels (sizes not identified) form the major part of their diet (Feare, 1970). This suggests that the preferences described herein for newly hatched *N. emarginata* may be of broader occurrence among intertidal thaidine gastropods.

Clearly, strong prey species and size preferences can be established without prior foraging experience even in species, such as *N. emarginata*, which use such experience later in life to make foraging decisions. In fact, newly hatched *N. emarginata* are considerably more selective than has been reported for late juvenile and adult *N. emarginata* (Palmer, 1984) or for late juveniles and adults of other thaidine gastropods (Hughes and Dunkin, 1984a; Palmer, 1984; West, 1986; Brown and Richardson, 1987; Gosselin and Bourget, 1989). It may seem surprising that food preferences can be highest before foraging experience is acquired in an animal that is known to use such experience later in life to enhance foraging efficiency. However, the range of prey species and sizes most preferred by an animal might be independent of experience early in life if the adaptive reason for selecting prey changes during ontogeny, as is discussed below.

2. Prey preferences and energy maximization

An important assumption of the energy maximization hypothesis is that the growth potential of a food type is a good indicator of its fitness value to the consumer (Charnov, 1976; Hughes, 1979; Palmer, 1983). Growth rate has indeed been shown to be related to fitness attributes in *Nucella emarginata* (Palmer, 1983). In this study, however, the preferred prey, *Mytilus* spp., did not promote faster growth in hatchling *Nucella emarginata* than did *Balanus glandula* or *Chthamalus dalli*. Prey energy density measurements, which allow within- and among-species comparisons of energy content for a given body size, were consistent with growth measurements: no significant difference in energy density was found between *Mytilus* and *Chthamalus*.

Lasaea spp., the only prey species on which hatchling growth was found to be significantly slower, contained less energy per unit body volume than *Mytilus* and *Chthamalus*. *Lasaea* is nevertheless occasionally consumed by hatchlings in the field (chapter II), perhaps because of its considerable abundance in microhabitats used by hatchlings (up to 1957 *Lasaea* / 100 cm^2 in *Semibalanus cariosus* microhabitats, chapter IV). Hatchlings might encounter several *Lasaea* without encountering other prey, and since searching for prey may be time consuming due to the slow crawling speed (chapter IV), hatchlings would occasionally attack *Lasaea* despite their lower energetic value.

Mussel size preferences might have conformed with the energy maximization hypothesis. The growth potential of different sizes of *Mytilus*, however, were not examined because the preferred mussel size undoubtedly changes as the snail grows. Nevertheless, energy density of mussels did not differ between size classes suggesting that the strong preference for the smallest *Mytilus* may have provided little energetic benefit relative to slightly larger *Mytilus*.

Hatchlings were able to drill *Mytilus* slightly faster than similar sized *Balanus* and *Chthamalus*, and the proportion of successful attacks after 48 hours was correspondingly higher on *Mytilus* (Fig. V-5b). No relationship was apparent, however, between drilling time and growth. Hatchlings grew as fast when feeding on *Balanus* and *Chthamalus* as did those feeding on *Mytilus* spp. (Fig. V-3). This may be because hatchlings are limited in the number of prey they can consume over short periods. Bayne and Scullard (1978a) determined that the time between two consecutive attacks (post-feeding phase) by *N. lapillus* was inversely related to snail size. The post-feeding phase in 8.5 mm snails, the smallest snails in their study, lasted at least three days, while time required to drill and ingest the prey (mussels) was three to five days. If the post-feeding phase in *N. emarginata* hatchlings is also long relative to drilling, the longer drilling time required for barnacles could be offset by using shorter intervals between attacks. However, *N. emarginata* hatchlings require at least 22 hours to drill, consume, and discard a small mussel (1 - 2 mm) (unpubl. data); drilling through the shell only requires 8 - 12 hours, and therefore extracting the prey's flesh requires at least as much time as drilling. For the prey sizes examined, differences in required drilling time among prey species are therefore moderate relative to overall handling time. In addition, the energetic cost of drilling may be small relative to basic metabolism or to other activities such as ingestion (Bayne and Scullard, 1978b). Overall, the consequences of differences in drilling time on growth appear to be minimal. Consequently, these results suggest: i) that drilling time is a poor indicator of total energetic costs associated with attacking a prey item, or ii) that total costs are minimal and have little consequences for growth. Total drilling and ingestion time may nevertheless indicate risk of mortality or disturbance if snails in the field are exposed to increased danger or interference by competitors while positioned on a prey, consistent with the time minimization hypothesis (Menge, 1974; Hughes, 1980).

Hatchlings did not grow faster when provided with a variety of prey species (Fig. V-3), which is consistent with the hypothesis that *N. emarginata* have little or no need to complement their nutrient uptake by feeding on more than one species (Palmer, 1983).

Previous studies have identified three possible patterns of prey selection: non-selective, frequency dependent, and energy maximization (Palmer, 1984, and references therein). These patterns are based on differences in the importance of ingestive conditioning (Wood, 1968; Morgan, 1972) or of energetic considerations on choice of food type. Although physiological constraints and risk of predation, competition, or physiological stress may also influence prey preferences (e.g. by favouring prey that minimize handling time), these generally act to reduce selectiveness by increasing the use of prey providing inferior energetic returns (Menge, 1974; Lima and Dill, 1990; Burrows and Hughes, 1991a, b). The present results on hatchling growth and energy content of prey indicate that *Mytilus* spp., *Balanus*, and *Chthamalus* are of similar energetic value to the hatchlings; if hatchlings select prey exclusively based on considerations of energy gain, they should show no preference among these three species. This is not the case. In fact, their strong preference for *Mytilus* over *Balanus* and *Chthamalus* does not comply to either of the above three patterns: feeding was highly selective, was not a result of ingestive conditioning (these hatchlings had never even encountered prey), and did not favour prey based on ranking of energy return, with the exception of *Lasaea*. Clearly, other factors not yet considered can also produce strong food preferences.

3. Prey used as cues to locate protective microhabitats

Newly hatched *Nucella emarginata* can feed on at least six species of invertebrates that co-occur with the hatchlings in the field (chapter II). Of these, small *Mytilus* spp. (<5 mm shell length) and *Lasaea* are the only ones to be abundant and almost exclusively found within the same microhabitats as *N. emarginata* hatchlings when most hatchlings are present in the field (late spring to early fall, chapter IV). *Lasaea*, however, are of lower energetic value to hatchlings than *Mytilus*. In addition, *Lasaea* are most abundant among dense assemblages of *Semibalanus cariosus*, the least effective shelter of the three hatchling microhabitats, while small *Mytilus* spp. (≤5 mm shell length) are most abundant in tufts of *Cladophora columbiana*, the most effective shelter (chapter IV). The strong preference for very small *Mytilus* could therefore keep the young snails within protective microhabitats once these sites have been reached. If hatchlings are capable of locating prey from a distance, small *Mytilus* spp. could even be used as reliable cues to help the hatchlings locate havens in an otherwise highly dangerous environment (chapter III). Predatory marine gastropods are known to locate prey by following prey odours (Kohn, 1961; Wood, 1968; Morgan, 1972; Palmer, 1984), and even newly hatched muricid snails respond to prey odours (*Urosalpinx cinerea*, Williams et al., 1983).

Although this is possibly the first time prey preferences have been suggested as an adaptation in marine animals for locating structural refugia, planktonic larvae settling in benthic habitats have long been known to use established plants or animals, such as conspecifics, prey, or even predators, as cues for locating favourable sites (see review by Rodriguez et al., 1993). For newly hatched *N. emarginata*, conspecifics would be poor indicators of the location of protective microhabitats because late juveniles and adults are often out on open surfaces (chapter IV), and hatchlings are usually sparsely distributed (≈1 - 5 ind. / 100 cm^2, unpubl. data). Densities of small *Mytilus* spp., however, can reach 2056 ind. / 100 cm^2 within protective microhabitats (chapter IV) and may therefore constitute effective cues for locating those refuges, or at least contribute to keeping the hatchlings therein once they have entered.

Early juvenile *Mytilus* spp. probably use such refugia for the same reasons as hatchlings (i.e. to avoid desiccation, predators, and dislodgement by waves; also see Petersen, 1984). For these small *Mytilus*, the risk of being killed by hatchlings is probably small relative to the risk of mortality on open surfaces.

If early juvenile *N. emarginata* do use small *Mytilus* as cues to locate protective microhabitats, the gradual shift in microhabitat use from structural refugia to open surfaces over the sizes of 3 - 8 mm shell length (chapter VI) should correspond to a shift in prey preferences. Prey preferences do change at some point during ontogeny, as late juvenile and adult *N. emarginata* preferentially consume mid-sized *Balanus* (Palmer, 1984), which mostly located on open surfaces. In addition, prey preferences in late juvenile and adult *N. emarginata* (Palmer, 1984) and *N. lapillus* (Hughes et al., 1992) are only moderate or weak compared to the preferences of newly hatched *N. emarginata*.

Since hatchlings may not survive one full tidal cycle if not located in protective microhabitats (chapter IV), this intense selective pressure could explain why prey species and size preferences are so strong at the onset of independent benthic life. For example, a preference of early juveniles for barnacles, mainly located on open surfaces, would result in a substantially reduced likelihood of survival, while a preferrence for prey other than the preferred prey type by late juvenile and adult snails would only result in smaller net energy gains (cf. Palmer, 1983, 1984; Brown and Richardson, 1987; Hughes and Burrows, 1990, 1991a).

Alternatively, hatchlings may use other cues to locate protective microhabitats, or the distribution of hatchlings may be a result of differential mortality with no active selection of microhabitat. In any case, considerations of energy gain can not explain the strong preference of hatchlings for small mussels. Although such a strong prey preference is likely to be adaptive, further studies of the responses of hatchlings to prey odours and on ontogenetic changes in prey preferences are necessary to fully understand the significance of prey selection. Such research may provide an understanding of the mechanisms controlling the distribution of predatory snails throughout ontogeny.

References

Bayliss, D.E. 1982. Switching by *Lepsiella vinosa* (Gastropoda) in South Australian mangroves. Oecologia. 54: 212-226.

Bayne, B.L. and C. Scullard. 1978a. Rates of feeding by *Thais (Nucella) lapillus* (L.). J. Exp. Mar. Biol. Ecol. 132: 113-129.

Bayne, B.L. and C. Scullard. 1978b. Rates of oxygen consumption by *Thais (Nucella) lapillus* (L.). J. Exp. Mar. Biol. Ecol. 132: 97-111.

Brown, K.M. and T.D. Richardson. 1987. Foraging ecology of the southern oyster drill *Thais haemastoma* (Gray): constraints on prey choice. J. Exp. Mar. Biol. Ecol. 114: 123-141.

Burrows, M.T. and R.N. Hughes. 1991a. Optimal foraging decisions by dogwhelks, *Nucella lapillus* (L.): influences of mortality risk and rate-constrained digestion. Funct. Ecol. 5: 461-475.

Burrows, M.T. and R.N. Hughes. 1991b. Variation in foraging behaviour among individuals and populations of dogwhelks, *Nucella lapillus*: natural constraints on energy intake. J. Anim. Ecol. 60: 497-514.

Charnov, E. 1976. Optimal foraging: attack strategy of a mantid. Am. Nat. 110: 141-151.

Derby, C.D. and J. Atema. 1981. Selective improvement in responses to prey odours by the lobster *Homarus americanus* following feeding experience. J. Chem. Ecol. II: 1073-1080.

Feare, C.J. 1970. Aspects of the ecology of an exposed shore population of dogwhelks *Nucella lapillus* (L.). Oecologia. 5: 1-18.

Gosselin, L.A. and E. Bourget. 1989. The performance of an intertidal predator *Thais lapillus*, in relation to structural heterogeneity. J. Anim. Ecol. 58: 287-303.

Hughes, R.N. 1979. Optimal diets under the energy maximization premise: the effects of recognition time and learning. Am. Nat. 113: 209-221.

Hughes, R.N. 1980. Optimal foraging in the marine context. Oceanogr. Mar. Biol. Ann. Rev. 18: 423-481.

Hughes, R.N. and M.T. Burrows. 1990. Energy maximisation in the natural foraging behaviour of the dogwhelk, *Nucella lapillus*. In: Trophic Relationships in the Marine Environment. Proc. 24th Europ. Mar. Biol. Symp. Eds. M. Barnes and R.N. Gibson. Aberdeen University Press, Aberdeen, UK. pp. 517-527.

Hughes, R.N. and M.T. Burrows. 1991. Diet selection by dogwhelks in the field: an example of constrained optimization. Anim. Behav. 42: 47-55.

Hughes, R.N., M.T. Burrows, and S.E.B. Rogers. 1992. Ontogenetic changes in foraging behaviour of the dogwhelk *Nucella lapillus* (L.). J. Exp. Mar. Biol. Ecol. 155: 199-212.

Hughes, R.N. and S. de B. Dunkin. 1984a. Behavioral components of prey selection by dogwhelks, *Nucella lapillus* (L.), feeding on mussels, *Mytilus edulis* L., in the laboratory. J. Exp. Mar. Biol. Ecol. 77: 45-68.

Hughes, R.N. and S. de B. Dunkin. 1984b. Effect of dietary history on selection of prey, and foraging behaviour among patches of prey, by the dogwhelk, *Nucella lapillus* (L.). J. Exp. Mar. Biol. Ecol. 79: 159-172.

Johnson, R.A. 1991. Learning, memory, and foraging efficiency in two species of desert seed-harvester ants. Ecology. 72: 1408-1419.

Kohn, A.J. 1961. Chemoreception in gastropod molluscs. Amer. Zool. 1: 291-308.

Largen, M.J. 1967. The diet of the dog-whelk, *Nucella lapillus* (Gastropoda Prosobranchia). J. Zool. (Lond.). 151: 123-127.

Lima, S.L. and L.M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68: 619-640.

Lowenstam, H.A. and S. Weiner. 1989. On Biomineralization. Oxford University Press, Oxford, UK. 324 p.

McEdward, L.R. and S.F. Carson. 1987. Variation in egg organic content and its relationship with egg size in the starfish *Solaster stimpsoni*. Mar. Ecol. Prog. Ser. 37: 159-169.

Menge, J.L. 1974. Prey selection and foraging period of the predacious rocky intertidal snail, *Acanthina punctulata*. Oecologia. 17: 293-316.

Morgan, P.R. 1972. *Nucella lapillus* (L.) as a predator of edible cockles. J. Exp. Mar. Biol. Ecol. 8: 45-52.

Palmer, A.R. 1983. Growth rate as a measure of food value in thaidid gastropods: assumptions and implications for prey morphology and distribution. J. Exp. Mar. Biol. Ecol. 73: 95-124.

Palmer, A.R. 1984. Prey selection by thaidid gastropods: some observational and experimental field tests of foraging models. Oecologia. 62: 162-172.

Palmer, A.R. 1985. Genetic basis of shell variation in *Thais emarginata* (Prosobranchia, Muricacea). I. Banding in populations from Vancouver Island. Biol. Bull. 169: 638-651.

Palmer, A.R. 1990. Predator size, prey size, and the scaling of vulnerability: hatchling gastropods vs. barnacles. Ecology. 71: 759-775.

Palmer, A.R., S.D. Gayron, and D.S. Woodruff. 1990. Reproductive, morphological, and genetic evidence for two cryptic species of Northeastern Pacific *Nucella*. Veliger. 33: 325-338.

Parsons, T.R., Y. Maita, and C.M. Lalli. 1984. A manual of chemical and biological methods for seawater analysis. Pergamon, New York.

Petersen, J.H. 1984. Establishment of mussel beds: attachment behaviour and distribution of recently settled mussels (*Mytilus californianus*). Veliger. 27: 7-13.

Pyke, G.H., H.R. Pulliam, and E.L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Quart. Rev. Biol. 52: 137-154.

Rittschof, D., D. Kieber, and C. Merrill. 1984. Modification of responses of newly hatched snails by exposure to odours during development. Chem. Sens. 9: 181-192.

Rodriguez, S.R., F.P. Ojeda, and N.C. Inestrosa. 1993. Settlement of benthic marine invertebrates. Mar. Ecol. Prog. Ser. 97: 193-207.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. W.H. Freeman and Co., New York, NY, Second edition. 859 pp.

Spight, T.M. 1975. On a snail's chances of becoming a year old. Oikos. 26: 9-14.

Vermeij, G.J. 1972. Interspecific shore-level size gradients in intertidal molluscs. Ecology. 53: 693-700.

Vermeij, G.J. 1978. Biogeography and Adaptation. Patterns of Marine Life. Harvard University Press, Cambridge, Massachussetts, USA. 332 p.

Vermeij, G.J. 1987. Evolution and Escalation. An Ecological History of Life. Princeton University Press, Princeton, New Jersey, USA. 527 p.

Werner, E.E. and J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst. 15: 393-425.

West, L. 1986. Interindividual variation in prey selection by the snail *Nucella* (*=Thais*) *emarginata*. Ecology. 67: 798-809.

Williams, L.G., Rittschof, D., B. Brown, and M.R. Carriker. 1983. Chemotaxis of oyster drills *Urosalpinx cinerea* to competing prey odours. Biol. Bull. 164: 536-548.

Wood, L. 1968. Physiological and ecological aspects of prey selection by the marine gastropod *Urosalpinx cinerea* (Prosobranchia, Muricidae). Malacologia. 6: 267-320.

CHAPTER VI

Conclusion:
Are hatchling snails simply small adults?

Introduction

The early juvenile period of most benthic marine invertebrates remains a period of life that has received little attention. Details of the ecology of the early juvenile period are sparse and have mainly been acquired through studies of sessile organisms (Keough and Downes, 1982; Young and Chia, 1984; Connell, 1985) or motile organisms in subtidal habitats (e.g. Sarver, 1979; Caddy, 1986; Rowley, 1989). After metamorphosis, early juveniles are morphologically different from larvae, but often resemble adults. If early juveniles are also ecologically similar to adults, one would only have to study the adults to identify the mechanisms regulating the distribution and abundance of organisms from the onset of independent benthic life. In terms of their ecology, early juveniles would in essence be small adults. But is this the case?

Differences do exist between early juveniles and adults. The most apparent is size. Most benthic organisms begin independent benthic life as members of the smaller meiofauna (Thorson, 1966), but subsequent increases in body size may span over four orders of magnitude (e.g. lobsters: Wolff, 1978; and mussels: Suchanek, 1981). Size is an important determinant of the nature and outcome of interactions with the environment (Schmidt-Nielsen, 1984); growth can therefore be responsible for other ontogenetic changes. For example, vulnerability to desiccation (Foster, 1971; Vermeij, 1972; Wolcott, 1973) and predation (Vermeij, 1972, 1987) scale inversely with size. An additional difference between early juveniles and adults is experience. At the onset of independent benthic life, early juveniles have little or no knowledge of their immediate surroundings and must therefore rely on pre-established response patterns or on very limited information. Adults, however, may have acquired considerable information on their environment and use this information when making decisions (e.g. Wood, 1968; Dunkin and Hughes, 1984).

A detailed comparison of early juveniles and adults is therefore necessary to determine if the ecology of an organism remains the same after the onset of independent benthic life, or if the differences are such that early juveniles and adults are in fact ecologically distinct.

A case study: *Nucella emarginata*

Sufficient information is now available for a detailed comparison of early juveniles and adults of the intertidal muricid gastropod, *Nucella emarginata* (Deshayes) (northern) (cf. Palmer et al., 1990). I review here available information on body size, experience, feeding, mortality factors, distribution, and shell coloration.

i) Body size

Female *Nucella emarginata* produce benthic egg capsules from which individuals emerge after ≈60 days as crawl-away juveniles. At the time of emergence, average size is ≈1.2 mm shell length (Spight, 1976; unpubl. data), while adult sizes often reach 25 mm or more (Spight, 1975; appendix 1), an increase in shell length (SL) of at least 20.8 times. Over this size range, body weight increases by ≈6700 times (based on shell length vs. whole weight regression using data from Palmer, 1982).

ii) Experience

Newly hatched snails would have little information on the habitat in which they will live. Odours may penetrate the egg capsule during development, providing some information to the embryos (e.g. *Urosalpinx cinerea*, Williams et al., 1983). However, the usefulness of such information to the hatchling is uncertain (see chapter IV). In addition, the odours must diffuse through the capsule walls and intracapsular fluid before reaching the embryos, and therefore the strongest, most persistent odours are the ones most likely to be detected. Odours that occur as pulses (e.g. when a motile predator passes nearby) may be undetected or be retained in the capsule for extended periods, providing a potentially biased perception of the environment. At the time of emergence from the egg capsule, the young juvenile does not have the benefit of experience from prior contact with substrata or prey, or from direct exposure to local weather and hydrodynamic conditions. Since *N. emarginata* can live at least two years (Spight, 1982;

Gosselin, unpubl. data), individuals have time to explore and acquire information on the habitat in which they live. Adults of the genus *Nucella* do rely on experience when making decisions (e.g. when selecting prey: Morgan, 1972; Dunkin and Hughes, 1984; Palmer, 1984a). While adults make "informed decisions" regarding the way they interact with their environment, newly hatched individuals are most likely to rely on pre-established response patterns (chapter V) or depend on very limited information.

iii) Feeding

Hatchling and adult *N. emarginata* will feed on mussels (*Mytilus* spp.) and barnacles (*Balanus glandula* and *Chthamalus dalli*) (chapter II), but hatchlings will also feed on the bivalves *Musculus taylori* and *Lasaea* spp., which are not consumed by adults. Adult *N. emarginata* will also ignore *Mytilus* spp. smaller than 5 mm (chapter II). Hatchlings, on the other hand, strongly prefer very small *Mytilus* (1 - 2 mm SL) (chapter V).

Both hatchlings and adults actively select their prey, but they do so for different reasons (chapter V). Late juvenile and adult *N. emarginata* prefer mid-sized barnacles (*Balanus glandula*), which maximize the net rate of energy intake (Palmer, 1984a). Considerations of energy gain, however, can not explain the strong preference of hatchlings for small mussels (*Mytilus* spp.) over barnacles (chapter V). Instead, hatchling prey preferences might be an adaptation that directs the young snails to protective microhabitats in which most small mussels are located (chapters IV and V).

iv) Mortality factors

The vulnerability of hatchling and adult snails to desiccation and predators contrast sharply. Newly hatched *N. emarginata* are highly vulnerable to desiccation: hatchlings exposed to drying conditions suffer 100% mortality within two to four hours (chapter III), and are therefore unable to survive direct exposure to desiccation for the duration of a single low tide in their natural habitats. Adults are much more resistant to desiccation, and can undoubtedly withstand most drying conditions occurring within the range of tidal heights they occupy without suffering mortality.

Hatchling and adult *N. emarginata* also have distinct sets of predators. Hermit crabs (*Pagurus* spp.) and shore crabs (*Hemigrapsus nudus*) appear to be the only important predators of early juvenile *N. emarginata* (chapter III). The abundance of these predators is nevertheless considerable at many sites, and undoubtedly constitute a formidable threat to early juveniles. Intertidal *Pagurus* species are nevertheless unable to kill adult snails, and although the largest *H. nudus* are capable of killing small adults (≤17 mm SL), such large *H. nudus* seldom occur in habitats used by *N. emarginata* (chapter III). The main predators of adult snails, the crab, *Cancer productus*, and the seastar, *Pisaster ochraceus*, will not feed on hatchlings (chapter III). Survival through the early juvenile period thus appears to depend mainly on avoiding mortality factors which seldom constitute a threat to adults.

v) Distribution

Although most *Nucella emarginata* probably spend their entire life within a few meters of the site where their egg capsule are deposited (Palmer, 1984b; chapter IV), ontogenetic shifts in distribution do occur. Early juveniles are almost exclusively located within three structurally complex microhabitats: filamentous algae (*Cladophora columbiana*), mussel clusters (*Mytilus californianus* and *M. trossulus*), and dense assemblages of large barnacles (*Semibalanus cariosus*). These microhabitats provide protection from desiccation and predation, and their use is essential for survival through this period. Most adults, however, are conspicuously located on open surfaces (chapter IV).

vi) Shell coloration

Hatchlings and adults bear contrasting shell colorations. The shells of newly hatched *N. emarginata* are uniformly white (pers. obs.). Adults, however, may be of a variety of colours (brown, orange, grey, or black) or patterns (banded or uniform) (Palmer, 1984b; 1985) but are rarely white.

In summary, early juvenile *N. emarginata* are smaller than adults, in terms of body mass, by more than three orders of magnitude, are much less experienced, are considerably more vulnerable to desiccation, are killed by a different set of predators, use different food and microhabitat resources, and bear distinct shell colorations. These characteristics indicate considerable differences in selective pressures and adaptive traits, and constitute significant ontogenetic changes in the relationship of the organism with its environment. Hence, the early juvenile period is clearly an ecologically distinct stage of life in *N. emarginata*.

Ecological transitions

The recognition of the early juvenile period as a distinct stage of life will provide significant insight only if we can define the period of life during which the juvenile's relationship with its environment remains relatively constant. In *Nucella emarginata*, the early juvenile stage starts with an abrupt shift when the individual emerges from its egg capsule and begins independent benthic life. The end of the early juvenile stage will also be characterized by an ecological transition, but it is not known whether this occurs as an extended, gradual transition, or as an abrupt shift. Consequently, the following study was carried out in order to document the transition period marking the end of the early juvenile stage in *N. emarginata*. Specifically, the objectives were to examine the ontogeny of: 1) vulnerability to desiccation; 2) vulnerability to hatchling predators; 3) microhabitat use; and 4) coloration and elemental composition of the shell.

Materials and methods

1. Study site and organism

The observations and experiments presented herein were carried out at the Bamfield Marine Station and at nearby field sites in Barkley Sound on the west coast of Vancouver Island, British Columbia, Canada. Newly hatched *Nucella emarginata* were obtained by collecting ripe egg capsules (unplugged capsules containing metamorphosed individuals that have not yet emerged) from local field sites and placing them in cages in flowing seawater in the laboratory. Only the hatchlings that emerged during the first 24 hours in the laboratory were used, providing individuals of known, identical age (time of emergence is considered $t = 0$). All snails ≥ 2 mm SL were collected from Ross Islets

(48°52'35" N, 125°09'65" W). Prior to their use in the following experiments, all snails were continuously immersed in flowing seawater.

2. Ontogeny of vulnerability to desiccation

To determine when *Nucella emarginata* acquires the ability to withstand desiccation stress for the duration of a low tide period, snails of a range of sizes were exposed to a controlled environment simulating field conditions at low tide. The experiment was carried out in August 1992 within 24 hours of collecting the snails. Hatchlings for this experiment were collected from Kirby Point (48°50'85"N, 125°12'40"W). Size classes consisted of newly hatched snails (1.0 - 1.5 mm SL), larger juveniles (2.1 - 3.0 mm, 3.1 - 5.0 mm, and 6.5 - 9.0 mm SL), and adults (18.0 - 26.0 mm SL). The snails were placed on shale rock plates (40 x 40 x 3 cm) wetted with seawater in an incubator at 22 °C. This air temperature was typical of the intertidal zone at low tide in Barkley Sound on a warm day (chapter III). A fan in the incubator maintained a continuous, moderate air flow throughout the experiment. A separate set of each size class of snails were recovered after 1, 2, 4, 6, and 8 hours. Sample sizes for each observation interval were as follows: 1 - 1.5 mm = 15 snails; each other size class = 10 snails. Due to limited availability, however, only one set of 2 - 3 mm and 6.5 - 9 mm snails were used; these were recovered only at the end of the eight hour experiment. Once removed from the incubator, snails were immediately placed in flowing seawater for 30 minutes, after which each individual was examined. Individuals not responding when the operculum was touched with a probe were recorded as dead. Hatchlings dying from desiccation usually had darkened flesh and were easy to recognize. Approximate relative humidity was measured with a psychrometer at the start and end of the experiment.

3. Ontogeny of vulnerability to predators

Nucella emarginata of a range of sizes were offered to hatchling predators to determine when these predators cease to be a threat. Three steps were necessary to determine vulnerability: 1. Establish the relationship between predator size and the size range of snails they will consume; 2. Determine the size-frequency distribution of predators in the field; 3. Calculate a predation vulnerability index for each snail size based on the predator sizes present in *N. emarginata* habitats and the snail sizes these predators will consume.

3.1 Predator size - snail size relationship

To define the relationship between predator size and the maximum and minimum snail sizes they will consume, three hatchling predators (*Hemigrapsus nudus*, *Pagurus hirsutiusculus*, and *P. granosimanus*) of a broad range of sizes were collected in the intertidal zone from crevices, among boulders, and from under fucoid algae. These decapod crustaceans, particularly *P. hirsutiusculus* and *H. nudus*, constitute the most abundant and often the only predators likely to be an important threat to hatchling *N. emarginata* in Barkley Sound (chapter III). *H. nudus* and *P. granosimanus* were collected at Ross Islets; *P. hirsutiusculus* were collected at Kirby Point. The intertidal zone, including areas not populated by *N. emarginata*, was searched extensively to obtain the largest predators available. Predators with intact claws were brought to the laboratory, measured (claw length (CLL) and claw width (CLW)), and individually placed in cages (95 x 95 x 60 mm, with 610 μm mesh screening) in flowing seawater for three days before adding snails. *N. emarginata* were also collected and separated into 1 mm size classes. When not placed with predators, snails were kept in cages in a separate seawater tank with a supply of small mussels as food.

The predators were offered snails from 6 September to 26 October 1992. Snails and shell fragments remaining in each cage were recovered every two days and a new set of three snails were added. When a predator had killed at least one snail it was then offered snails of the next larger size class. If a predator had not killed any of the snails, it was offered a new set of snails of the same size a second time; the same size was offered a third time only if the predator seriously damaged the snails without killing them. The reverse procedure was used to determine the smallest *N. emarginata* that a given predator would kill.

Equations describing the relationships between predator size and consumed snail size were then determined by regression analysis. The experiment initially included 20 individuals of each predator species; some individuals moulted during the study, however, and their results could not be used. Predators that did not kill snails were not included in the regression analysis but were taken into consideration when calculating the index value.

3.2 Size-frequency distribution of hatchling predators in the field

The size-frequency distribution of hatchling predators in habitats populated by *Nucella emarginata* was assessed at Ross Islets, Wizard Islet, and Dixon Island (low-moderate, moderate, and moderate-high exposure to wave action, respectively). Predators were sampled between 16 August and 7 September 1993, a time when hatchling *N. emarginata* are usually present (appendix 2). Five quadrats (25 x 25 cm) were sampled at 1 m intervals along each of two transects running parallel to the shore at 1.2 to 1.8 m above mean lower low water (10 quadrats per site). The length of the right claw of each *Hemigrapsus nudus* and *Pagurus* spp. found within these quadrats was measured. Claws shorter than 9 mm were measured using the ocular micrometer of a dissecting microscope (±0.08 mm); larger claws were measured using a dial caliper (±0.1 mm). If the right claw was missing or was visibly smaller than the left one, the left claw was then measured. No measurements were taken on predators lacking both claws.

3.3 Predation vulnerability index

To determine when *Nucella emarginata* cease to be vulnerable to predators of hatchlings, a *predation vulnerability index* was calculated as a function of snail size. The index value for a given snail size consists of the density of hatchling predators that would feed on a snail of this size. The steps in assessing the value of the index for a given snail size were as follows: 1) the range of *H. nudus* sizes capable of feeding on snails of this size was calculated using the equations relating *H. nudus* size to the largest and smallest consumed snails; 2) field densities of *H. nudus* within this size range were determined based on size-frequency data for the field sites. The density of *H. nudus* was then reduced to account for the proportion of crabs that would not attack snails in the laboratory experiments; 3) the first two steps were repeated for each *Pagurus* species; and 4) the corresponding reduced densities of each predator species were totalled to produce the index value for the given snail size at one field site. The index value was calculated in this way for each of the three sites at which size-frequency distributions of predators had been assessed.

4. Ontogeny of microhabitat use

The body size at which the distribution of *Nucella emarginata* shifts from structurally complex microhabitats to open surfaces was determined by field observations at three sites. Observations were carried out along transects at Ross Islets in July 1992 and again in September 1993, at Wizard Islet in September 1991 and in August 1992, and at Cape Beale (48°47'20" N, 125°12'95" W), a site exposed to full ocean surge, in July 1992. Details of the sampling procedure are reported in chapter IV. Sampling was carried out when hatchlings and juveniles were known to be present based on previous field observations (appendix 2). The size (SL) and position of the snails within the sampled quadrats, whether on open surfaces or within complex microhabitats, were recorded.

5. Ontogeny of coloration and elemental composition of the shell

Changes in shell colour were documented from *Nucella emarginata* collected at Ross Islets on eight occasions in September and October 1992. Open surfaces were examined and structurally complex microhabitats (algae, mussel clusters, and large barnacles) were gently taken apart *in situ* or returned to the laboratory and thoroughly washed in freshwater to extract all snails smaller than 14 mm SL (the full size range of immature snails; see Palmer, 1985). Each snail was then measured and the shell colour (white, intermediate, or black) and pattern (banded or uniform) were recorded within 24 hours of collection. Brown, grey and orange shells were recorded as intermediate. Because new shell growth is deposited along the lip of the aperture, observations at this site will show when the snails begin to incorporate a different colour into their shell. The shell's appearance from the perspective of a nearby observer (or predator), however, will mostly remain unchanged until the new pigmentation reaches higher up on the main body whorl through continued growth. The colour and pattern were therefore examined on two areas of each shell: the outer lip of the aperture and the area of the main body whorl facing away from the substratum to which the snail is attached (top of whorl).

To determine if ontogenetic changes in pigmentation correspond to changes in elemental composition of the shell matrix, shells measuring 1 - 1.5 mm (newly hatched individuals, n = 3), 2 - 3 mm (n = 1), 5 - 6 mm (n = 1), and 10 - 11 mm (n = 1) in length were examined by energy dispersive x-ray analysis using a Cambridge Stereoscan 250 scanning electron microscope. This equipment detects elements contributing ≥1% of the material being analyzed.

Results

1. Ontogeny of vulnerability to desiccation

When exposed to desiccation, all snails ≤3 mm SL died within eight hours (Fig. VI-1). Survival increased with increasing size over the 3 - 6 mm SL size range: 30% of 3 - 5 mm snails were still alive after eight hours, but all snails ≥6 mm survived exposure to desiccation for the full duration of the experiment (Fig. VI-1). Relative humidity within the incubator decreased from 86% at the start of the experiment to 77% after eight hours; these values are comparable to levels observed in the intertidal zone at low tide (cf. chapter IV). The rock plates on which the snails were placed dried out after four to six hours, which corresponds to the period when the smallest snails died (Fig. VI-1).

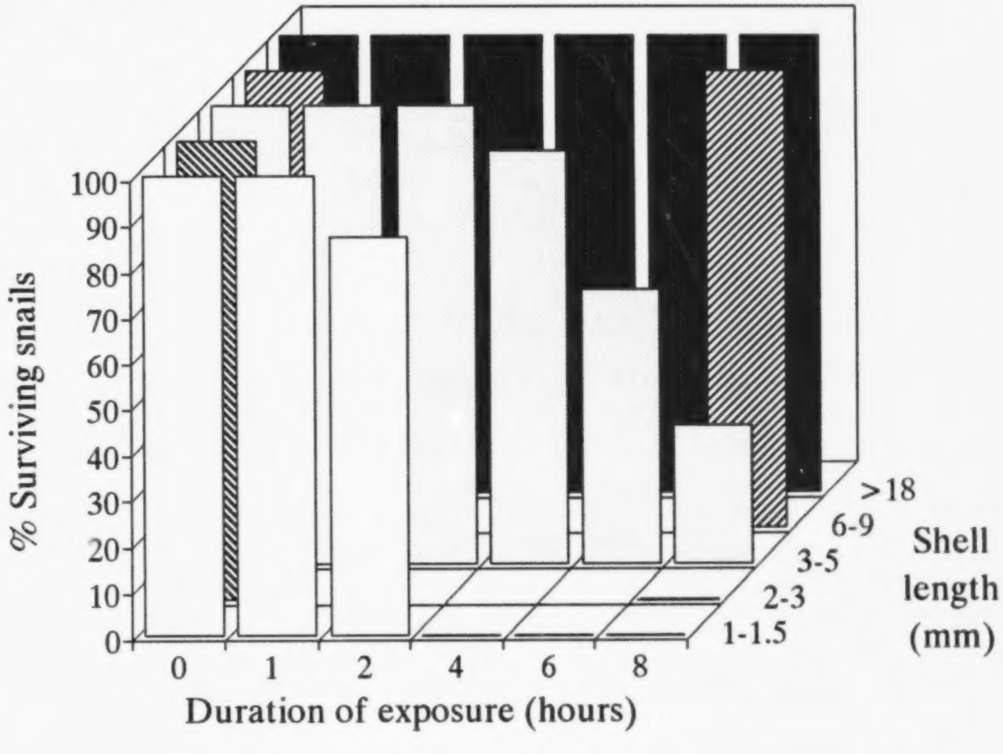
2. Ontogeny of vulnerability to predators

2.1 Predator size - snail size relationship

The size of the smallest snail killed did not scale with predator size. Even the largest *Pagurus hirsutiusculus* and *P. granosimanus*, as well as *Hemigrapsus nudus* measuring up to 19.2 mm CLL consumed newly hatched *Nucella emarginata*. Only the two largest *H. nudus*, 21.1 mm and 25.0 mm CLL, did not attack hatchlings.

The size of the largest snail killed did scale with predator size. For this relationship claw length measurements provided a better fit than claw width.

Figure VI-1. Survival time of *Nucella emarginata* emersed for up to eight hours at 22 °C as a function of shell length. After the treatment, all snails were placed in flowing seawater for 30 minutes before being examined for mortality. Each value represents the survival of a separate set of 1 - 1.5 mm (n = 15) or larger snail sizes (n = 10 per size class). For 2 - 3 and 6 - 9 mm size classes, survival was determined only for the full eight hour exposure period.


% Surviving snails
100
90
80
70
60
50
40
30
20
10
0
0
1
2
4
6
8
Duration of exposure (hours)
>18
6-9
3-5
2-3
1-1.5
Shell length (mm)

The correlation was also improved by using log transformations of predator and prey sizes. The regression equations between CLL and largest snail killed were highly significant ($p \leq 0.001$) for *H. nudus* and *P. hirsutiusculus* (Fig. VI-2a, b). Many *P. granosimanus* only attacked the smallest snails, producing a poor fit between CLL and the size of the largest consumed snail. Consequently, only three data points were used to calculate the regression between CLL and largest snail killed (Fig. VI-2c). The proportion of *P. granosimanus* not attacking snails >1.5 mm was taken into account, however, when calculating the predation vulnerability index.

These predators used different methods to gain access to the flesh of the snails. *P. granosimanus* chipped the shells such that the remaining shells typically had a broken siphonal canal and the lip of the aperture chipped partway up the main body whorl. Snails slightly too large to be killed by *P. granosimanus* often had damaged shells. *P. hirsutiusculus*, on the other hand, crushed the shells into small fragments, and few damaged live snails remained after two days; marks and punctures were observed in the shells of a few uneaten snails but the lip of the aperture was never chipped. *H. nudus* also crushed most shells, but would chip the aperture lip of larger snails. On two occasions *H. nudus* removed the flesh of a large snail (13 - 14 mm and 15 - 16 mm SL) without damaging the shell. Hermit crabs did not kill snails without breaking the shell.

2.2 Size-frequency distribution of hatchling predators in the field

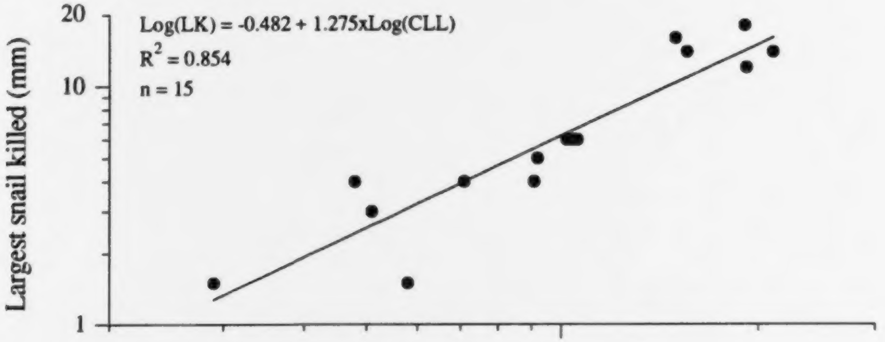
Within areas populated by *Nucella emarginata*, *Pagurus hirsutiusculus* was always the most abundant hatchling predator (Fig. VI-3); relatively few *P. granosimanus* and *P. samuelsis* were present. Predator densities were lowest at Dixon Island (also see chapter III), but the size range of predators was roughly similar at all sites. All *Pagurus* spp. were smaller than 9 mm CLL, and most were within the 1.1 - 5.0 mm size range (Fig. VI-3). *Hemigrapsus nudus* was always the largest predator, but did not exceed 15.9 mm CLL.

2.3 Predation vulnerability index

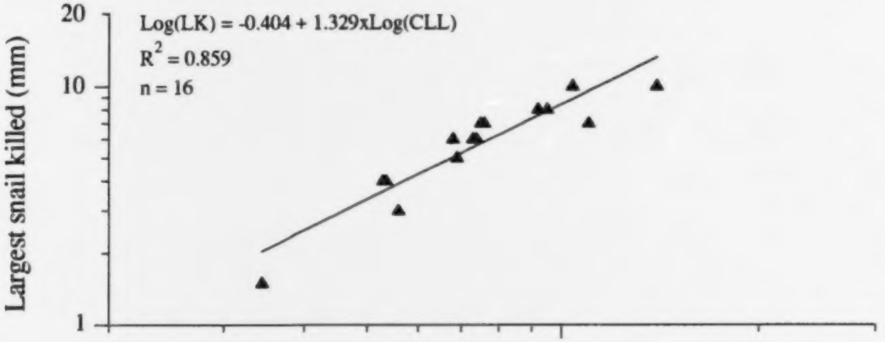
The predation vulnerability index decreased with increasing snail size, reaching zero for snails measuring ≥7.5 mm SL at Wizard, ≥8.0 mm at Ross, and ≥11.5 mm at

Figure VI-2. Relationship between log transformed predator claw length and size of largest *Nucella emarginata* killed. Because most *Pagurus granosimanus* only attacked newly hatched snails (≈1.5 mm shell length), the regression equation was calculated using only three values, indicated by circles (see text). All regression equations were significant ($p < 0.001$). LK: largest snail killed; CLL: claw length.

a) *Hemigrapsus nudus*



b) *Pagurus hirsutiusculus*



c) *Pagurus granosimanus*

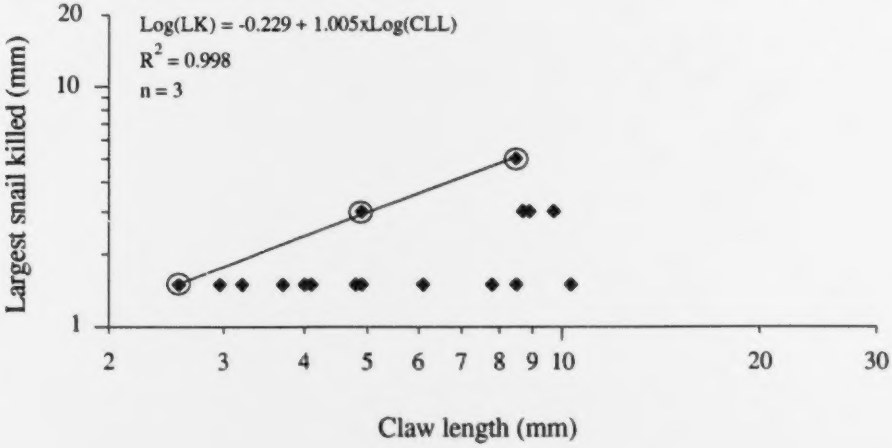
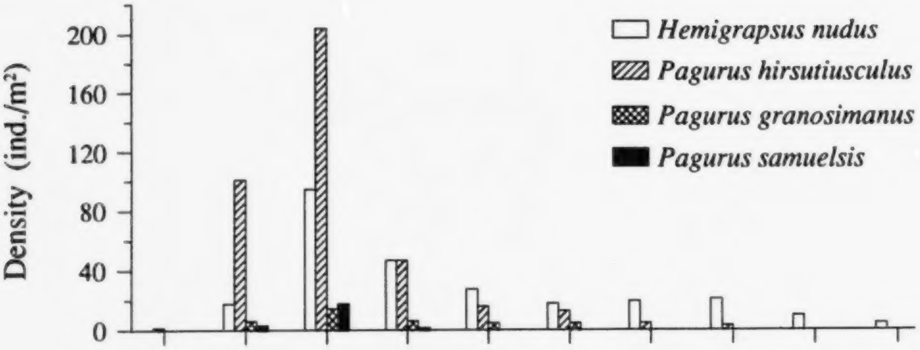
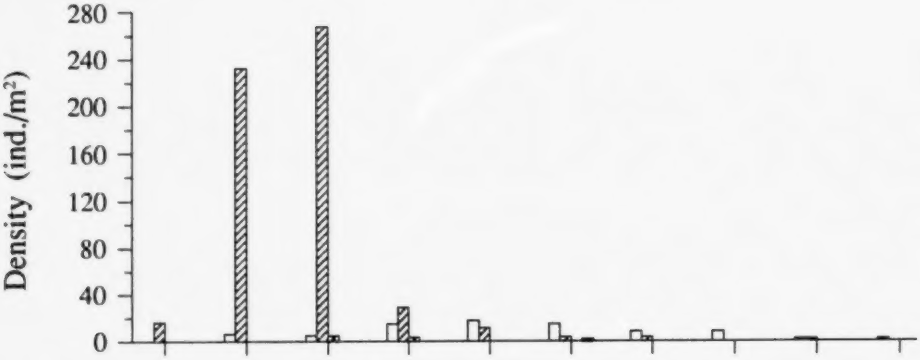


Figure VI-3. Size-frequency distribution of hatchling predators at three field sites in August and September 1993. Whenever possible, measurements were taken on the right claw of the predator. Each unit of the horizontal axis (claw length) represents the 1 mm interval preceding the listed value (e.g. 1.1 - 2.0 mm listed as 2 mm).

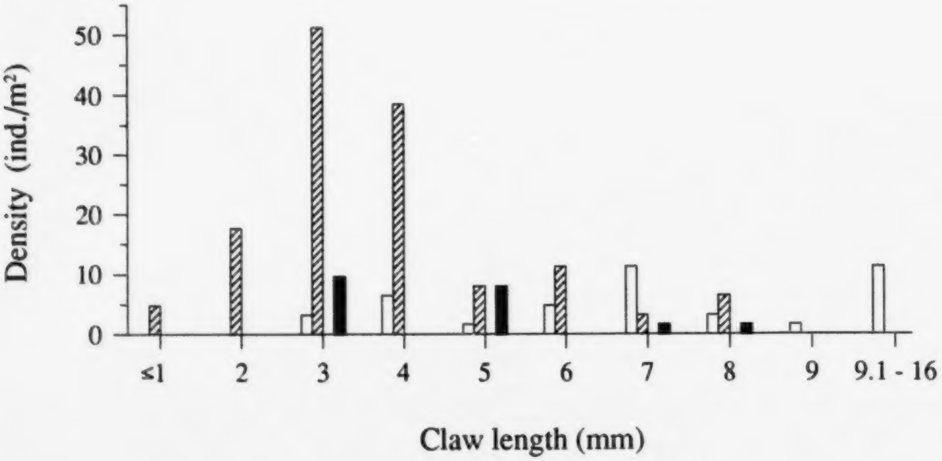
a) Ross Islets



b) Wizard Islet



c) Dixon Island



Dixon (Fig. VI-4). At these sizes, the snails have become invulnerable to hatchling predators.

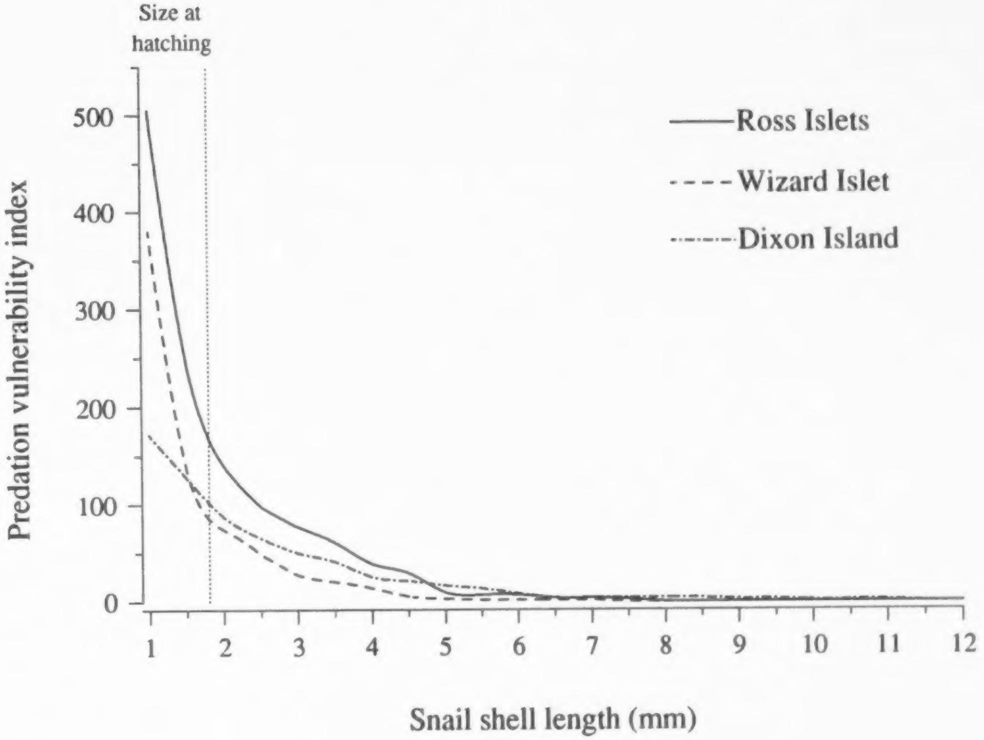
Adjustments were necessary when calculating the index to account for the proportions of predators large enough to kill snails but which would not do so in the laboratory experiment. The following adjustments are based on the assumption that predators in the field would attack or ignore snails in the same way as did those in the laboratory experiment, although this assumption may not be completely accurate (see discussion). In the *Hemigrapsus nudus* experiment, 21.1% of the crabs did not kill any snail, even though the smallest crab (2.9 mm CLL) did kill 1.0 - 1.5 mm and 2 - 3 mm snails. Densities of *H. nudus* were therefore reduced by 21.1% when calculating all index values. Among *Pagurus granosimanus* ≥4.9 mm CLL, 56.6% did not kill snails >1.5 mm SL (Fig. VI-2). Consequently, the following corrections were applied when calculating the contribution of this predator to the index value: for snails ≤1.5 mm SL: 100% x density of *P. granosimanus*; for snails >1.5 mm SL: 44.4% x density of *P. granosimanus*. No correction was needed for *P. hirsutiusculus*, and none was used for *P. samuelsis* based on observations of five *P. samuelsis* feeding on snails of various sizes.

The regression between claw size and consumed snail size was not determined for *P. samuelsis*. However, observations of shell fragments from snails killed by *P. samuelsis* suggest that this hermit crab crushes snail shells in the same way as *P. hirsutiusculus* does. The equation relating CLL to the largest snail killed for *P. hirsutiusculus* was therefore also used for *P. samuelsis* when determining the predation vulnerability index. Although this may reduce the accuracy of the results, this would only have a small effect on the index value because of the relatively low density of *P. samuelsis* at all sites.

3. Ontogeny of microhabitat use

The results from Ross, Wizard, and Cape Beale were pooled to obtain a detailed pattern of the distribution of juvenile *Nucella emarginata*. Separate results for each site are presented elsewhere (chapter IV). Although the total abundance of snails decreased with increasing snail size, somewhat obscuring changes in distribution, the shift in

Figure VI-4. Vulnerability of *Nucella emarginata* to hatchling predators as a function of shell length. The predation vulnerability index consists of the density (ind. / m^2) of all hatchling predators that would kill a snail of the given size. Index values were calculated for every 0.5 mm size increment, and the curves were then smoothed using the "spline curve" option of Sigma Plot® version 5.0 computer graphics program.


Size at hatching
Predation vulnerability index
500
400
300
200
100
0
1
2
3
4
5
6
7
8
9
10
11
12
Snail shell length (mm)
Ross Islets
Wizard Islet
Dixon Island

microhabitat use was nevertheless apparent (Fig. VI-5). A significant change in distribution occurred between the 2.1 - 3 mm and 3.1 - 4 mm sizes (Test of independence: $G_{adj} = 11.98$, $p < 0.005$, df = 1; G value adjusted using Williams' correction; Sokal and Rohlf, 1981). Over this size interval, the number of snails on open surfaces increased by 280%, while the number of snails in structurally complex microhabitats decreased by 56% over the same interval (Fig. VI-5). Snails >8 mm SL were mostly located on open surfaces, indicating that the transition from structurally complex microhabitats to open surfaces occurred over the 3 - 8 mm SL size range.

4. Ontogeny of coloration and elemental composition of the shell

The proportion of *Nucella emarginata* with entirely white shells decreased with increasing snail size up to 6 - 7 mm SL; only 1 out of 188 snails >6 mm was white. Non-white pigmentation was first observed in new shell growth among 2 - 3 mm snails (Fig. VI-6a). In most cases, these pigments were initially incorporated as very lightly coloured radial bands. The width of the bands and the density of the colour then gradually increased with snail size; often, the pigmented bands eventually merged and subsequent shell growth was uniformly coloured. The density of pigmentation also increased in most snails, in many cases becoming black. The proportions of each colour and pattern at the shell lip roughly levelled off among snails ≥6 mm SL (Fig. VI-6a).

Changes in the appearance of the snails, as apparent from the top of the body whorl, occurred at slightly larger sizes than at the aperture (Fig. VI-6b). The whorls of most 2 - 3 mm snails (79%) were still completely white. However, the proportions of each colour and pattern then changed rapidly up to the 7 - 8 mm size, and roughly levelled off among larger size classes (Fig. VI-6b). Changes in shell coloration therefore occurred mainly over the 3 - 7 mm SL size range.

No differences in elemental composition of the shell matrix were detected over the range of sizes that were analyzed (1.5 - 11 mm). In addition, the composition of recent shell growth was similar to that of older shell material on any given shell, including the first whorl produced while developing within the egg capsule. Shell material consisted mainly of calcium and trace amounts of aluminum, chlorine, magnesium, and sodium.

Figure VI-5. Distribution of *Nucella emarginata* ≤12 mm shell length (n = 353) on open surfaces or in structurally complex microhabitats. Pooled data from Ross Islet (1992 and 1993), Wizard Islet (1991 and 1992) and Cape Beale (1992).

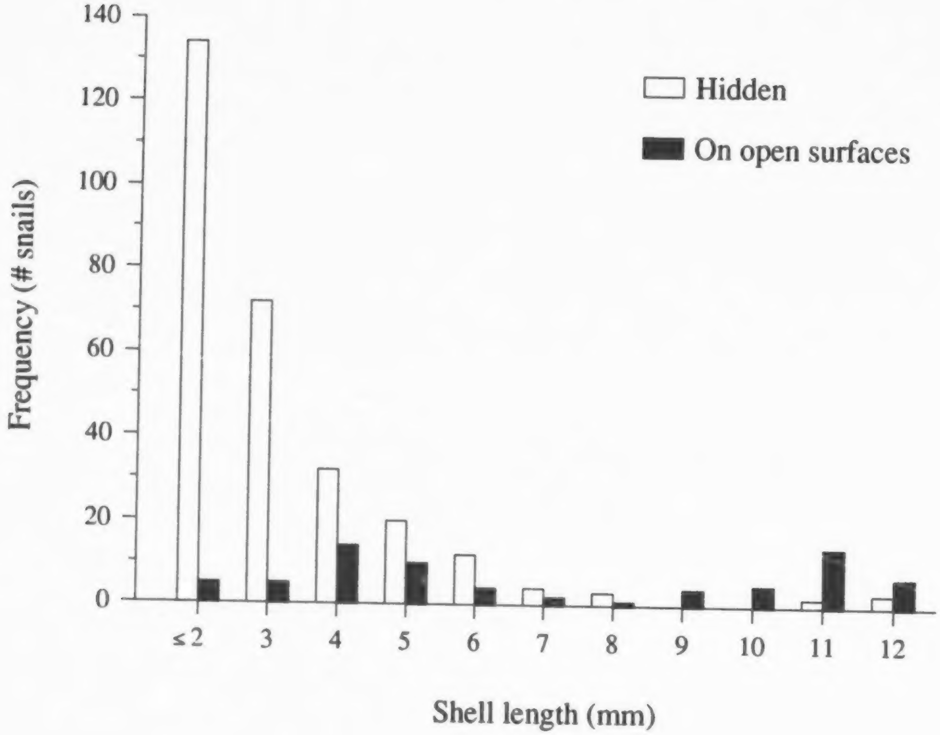
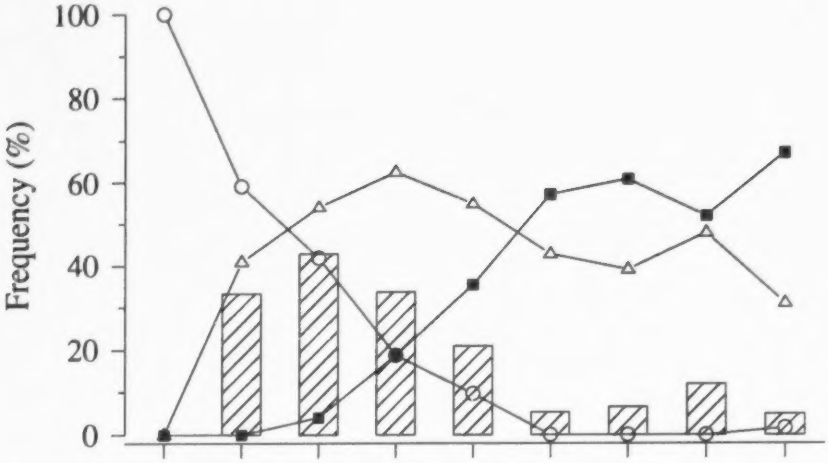
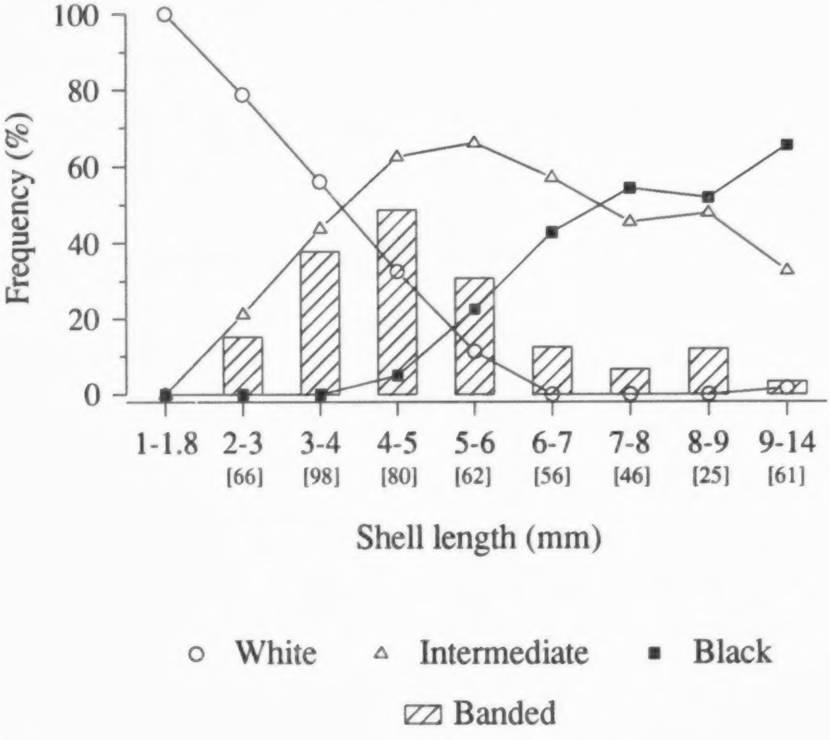

140
120
100
80
60
40
20
0
Frequency (# snails)
Hidden
On open surfaces
≤ 2
3
4
5
6
7
8
9
10
11
12
Shell length (mm)

Figure VI-6. Frequency of colour type and banded pattern on two areas of the shell of *Nucella emarginata* as a function of shell length. All snails were collected at Ross Islets in September and October 1992. Values in brackets are sample sizes for each size class. The "intermediate" category includes brown, orange, and grey colours.

a) Aperture lip



b) Top of whorl



Discussion

1. Desiccation

The ability to survive direct exposure to most desiccation conditions was acquired over the 3 - 6 mm SL size range. The smallest *Nucella emarginata* able to withstand relatively intense drying conditions for the equivalent duration of a low tide period were 3 - 5 mm SL (Fig. VI-1), and all snails ≥6 mm survived the treatment. More intense drying conditions, which even 6 - 9 mm snails might not survive, will occur in the field, although very infrequently (chapter III). Snails measuring 2 - 3 mm SL might have been less vulnerable to desiccation than 1 - 1.5 mm snails, but this reduced vulnerability was not sufficient for 2 - 3 mm snails to survive emersion for the duration of a low tide.

2. Predation

Vulnerability of *Nucella emarginata* to predators of hatchlings decreases gradually with increasing snail size; therefore, the onset of the transition period can not defined as a discrete size. Vulnerability is relatively low, however, for snails ≈4 mm SL, and snails become virtually invulnerable to hatchling predators once they reach 6.5 mm (Fig. VI-4).

The predation vulnerability index does not represent the exact intensity of predation on *N. emarginata* in the field, because it attributes an equal weight to each individual predator, and because the predation experiment was carried out in artificial settings. In fact, differences in willingness to feed on *N. emarginata* are likely to occur in the field among predator species and among predator sizes of a given species. Nevertheless, the index should constitute a good relative basis for comparisons among snail sizes.

The predation vulnerability index suggests an additional conclusion regarding size at hatching. Although the present study did not specifically examine changes over the range of hatching sizes (≈0.9 - 1.8 mm), thereby reducing the resolution of analysis over that size interval, the index nevertheless suggests a considerable reduction in vulnerability of hatchling *N. emarginata* to predators over this narrow size range (Fig. VI-4). Consequently, these results indicate that predation by decapod predators can constitute a strong selective pressure favouring a larger size at hatching at these sites, as has been suggested (Spight, 1976; Rivest, 1983), even though all newly hatched snails are vulnerable to these predator species. The sharp decline in vulnerability over the range of hatching sizes is a consequence of the size distribution of the predators, which was highly skewed towards small individuals, capable of killing only the smallest hatchlings, when the samples were collected. In addition, the gradient in vulnerability to predation differed from site to site (Fig. VI-4), suggesting that different populations may experience different levels of intensity of this pressure. If the among-site differences in predator population structure persist through time and if the selective pressure imposed by decapod predators is more intense than other pressures influencing size at hatching, then differences among sites in size at hatching should be predictable based on determinations of the predation vulnerability index. Further study of the correspondence between the predation vulnerability index and average size at hatching for several local populations over time are necessary before this relationship can be confirmed.

3. Microhabitat use

Nucella emarginata began appearing more often on open surfaces at the size of 3.1 - 4 mm SL, and occurred predominantly on open surfaces after reaching ≈8 mm (Fig. VI-5). This pattern was roughly the same at each of the three sites that were sampled (chapter IV), and is supported by field observations throughout four years of field work (1990-1993) in Barkley Sound. In addition, Spight (1975) regularly collected *N. emarginata* and *N. canaliculata* in Puget Sound, Washington, from 1967 to 1973, but rarely observed snails smaller than 5 mm SL among adults; most of the snails he collected were ≥10 mm SL. As discussed in chapter IV, it seems likely that the smallest snails were cryptically located in structurally complex microhabitats, and only emerged at a size slightly smaller than 10 mm SL. Hence, the shift in distribution over the 3 - 8 mm SL size range observed in the present study does not appear to be restricted to *N. emarginata* in Barkley Sound.

The proportion of large snails hidden in structurally complex microhabitats will undoubtedly correlate to some extent with the availability of structures large enough to conceal them. Many large snails nevertheless remain conspicuous on open surfaces even at sites where microhabitats capable of concealing them are abundant (e.g. extensive beds of large *Mytilus californianus* at Cape Beale; cf. chapter IV). The change in microhabitat use by *N. emarginata* thus represents an ontogenetic shift largely independent of microhabitat availability. Whether this shift is a consequence of changes in microhabitat preferences, in differential mortality, or of dislodgement and relocation of small individuals on open surfaces was beyond the scope of this study. However, the distribution of *N. emarginata* throughout ontogeny could be a consequence of prey preferences (chapter V), whereby early juveniles would seek small mussels that are mainly located in structurally complex microhabitats, but would eventually emerge onto open surfaces as a result of an increasing preference for barnacles (*Balanus glandula*).

4. Coloration and elemental composition of the shell

Most changes in appearance in *Nucella emarginata* occurred over the 3 - 7 mm SL size range (Fig. VI-6b). Snails <3 mm were mostly white, while all individuals >7 mm were either black, grey, brown, or orange. These changes did not correspond to detectable changes in the elemental composition of the shell.

Body coloration of aquatic organisms is often associated with differential mortality due to visual predators (Mercurio et al., 1985; Smith and Herrnkind, 1992; Vermeij, 1993). White hatchlings are indeed difficult to distinguish from white shell fragments and sand grains that accumulate in filamentous algae and mussel clusters, and from the fine-grained white surface of the shells of large barnacles. Decapod predators may use visual perception when foraging, but they are also known to locate prey by chemotaxis (Boulding and Hay, 1984; Zimmer-Faust, 1987). Other visual predators not yet identified, such as fish, may be responsible for the shift. Alternatively, shell colours may act to reduce physiological stress (e.g. Etter, 1988), or might even be non-adaptive, although the close correspondence between colour changes and shifts in vulnerability and distribution suggest otherwise. At present, the significance of ontogenetic changes in shell colour remains unclear.

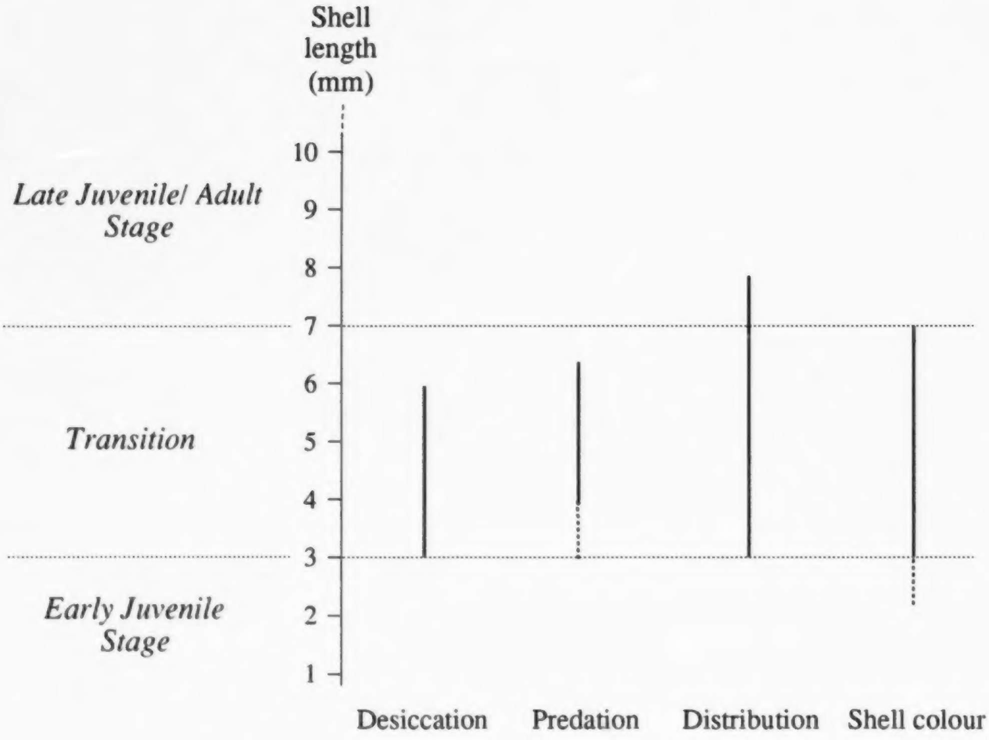
5. Duration of the early juvenile stage in *Nucella emarginata*

The ontogenetic changes examined in this study all occurred over approximately the same size range (Fig. VI-7). Vulnerability to mortality factors, distribution, and the colour of the shell remained homogeneous up to ≈3 mm SL. Snails then became increasingly capable of withstanding direct exposure to low tide desiccation conditions, and vulnerability to hatchling predators decreased to very low levels. As growing *N. emarginata* were then released from the restrictions imposed by desiccation and predation, the need to hide in microhabitats providing protection from these factors was also relaxed. The decrease in vulnerability to mortality factors was indeed mirrored by an increased frequency of occurrence of *N. emarginata* on open surfaces, as well as a gradual change in shell colour (Fig. VI-7).

The early juvenile stage in *N. emarginata* therefore lasts from the moment they emerge from their egg capsule until they reach ≈3 mm SL. *N. emarginata* then undergo a discrete ecological transition between the sizes of 3 - 7 mm SL, which constitutes the transition marking the end of the early juvenile stage. The transition period covers a broader range of sizes than the early juvenile stage, although each individual may complete changes in microhabitat use and shell colour over a narrow size range. *N. emarginata* thus appear to have three ecologically distinct stages: embryonic (encapsulated), early juvenile, and late juvenile/adult. Although a detailed comparison of late juveniles and adults might also conclude that they are ecologically distinct, this seems unlikely as few changes were observed beyond the size of 7 mm (chapter IV; this study).

In benthic marine organisms, mortality can be extremely high among early juveniles (Thorson, 1966; Branch, 1975; Sarver, 1979; Brawley and Johnson, 1991; Gosselin and Qian, submitted). Ontogenetic microhabitat shifts have been reported in lobsters (Wahle and Steneck, 1992; Smith and Herrnkind, 1992), scallops (Pohle et al., 1991), and nudibranchs (Sarver, 1979), and these shifts have been associated with

Figure VI-7. Summary of results for the four factors that were examined, showing the size interval over which the transition occurred.


Shell length (mm)
10
9
8
7
6
5
4
3
2
1
Late Juvenile/ Adult Stage
Transition
Early Juvenile Stage
Desiccation
Predation
Distribution
Shell colour

decreases in vulnerability to predators. Recent studies of lobsters inhabiting subtidal habitats (Wahle & Steneck, 1991; Smith & Herrnkind, 1992) have in fact concluded that early juveniles were ecologically distinct from adults, in agreement with the conclusions of the present study. Many benthic invertebrates increase considerably in size during post-larval life, and there is increasing evidence that ontogenetic shifts in microhabitat use are widespread among aquatic organisms with motile juveniles (Werner and Gilliam, 1984). It is therefore likely that the early juvenile period is also an ecologically distinct stage in most marine macrobenthic species with motile juveniles.

References

Boulding, E.G. and T.K. Hay. 1984. Crab response to prey density can result in density-dependant mortality of clams. Can. J. Fish. Aquat. Sci. 41: 521-525.

Branch, G.M. 1975. Ecology of *Patella* species from the Cape Peninsula, South Africa. IV. Desiccation. Mar. Biol. 32: 179-188.

Brawley, S.H. and L.E. Johnson. 1991. Survival of fucoid embryos in the intertidal zone depends on developmental stage and microhabitat. J. Phycol. 27: 179-186.

Caddy, J.F. 1986. Modelling stock-recruitment processes in Crustacea: some practical and theoretical perspectives. Can. J. Fish. Aquat. Sci. 43: 2330-2344.

Connell, J.H. 1985. The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. J. Exp. Mar. Biol. Ecol. 93: 11-45.

Dunkin, S. de B. and R.N. Hughes. 1984. Behavioural components of prey selection by dogwhelks, *Nucella lapillus* (L.), feeding on barnacles, *Semibalanus balanoides* (L.), in the laboratory. J. Exp. Mar. Biol. Ecol. 79: 91-103.

Etter, R.J. 1988. Physiological stress and color polymorphism in the intertidal snail, *Nucella lapillus*. Evolution. 42: 660-680.

Foster, B.A. 1971. Desiccation as a factor in the intertidal zonation of barnacles. Mar. Biol. 8: 12-29.

Gosselin, L.A. and P.-Y. Qian. Submitted. Early postsettlement mortality of intertidal barnacles: a critical period for survival. Ecology

Keough, M.J. and B.J. Downes. 1982. Recruitment of marine invertebrates: the role of active larval choices and early mortality. Oecologia. 54: 348-352.

Mercurio, K.S., A.R. Palmer, and R.B. Lowell. 1985. Predator-mediated microhabitat partitioning by two species of visually cryptic, intertidal limpets. Ecology. 66: 1417-1425.

Morgan, P.R. 1972. *Nucella lapillus* (L.) as a predator of edible cockles. J. Exp. Mar. Biol. Ecol. 8: 45-52.

Palmer, A.R. 1982. Growth in marine gastropods: a non-destructive technique for independently measuring shell and body weight. Malacologia 23: 63-73.

Palmer, A.R. 1984a. Prey selection by thaidid gastropods: some observational and experimental field tests of foraging models. Oecologia 62: 162-172.

Palmer, A.R. 1984b. Species cohesiveness and genetic control of shell color and form in *Thais emarginata* (Prosobranchia, Muricacea): preliminary results. Malacologia. 25: 477-491.

Palmer, A.R. 1985. Genetic basis of shell variation in *Thais emarginata* (Prosobranchia, Muricacea). I. Banding in populations from Vancouver Island. Biol. Bull. 169: 638-651.

Palmer, A.R., S.D. Gayron, & D.S. Woodruff. 1990. Reproductive, morphological, and genetic evidence for two cryptic species of Northeastern Pacific *Nucella*. Veliger 33: 325-338.

Schmidt-Nielsen, K. 1984. Scaling. Why is Animal Size so Important? Cambridge University Press, New York, New York, USA.

Pohle, D.G., V.M. Bricelj, and Z. Garcia-Esquivel. 1991. The eelgrass canopy: an - above-bottom refuge from benthic predators for juvenile bay scallops *Argopecten irradians*. Mar. Ecol. Prog. Ser. 74: 47-59.

Rivest, B.R. 1983. Development and influence of nurse egg allotment on hatching size in *Searlesia dira* (Reeve, 1846) (Prosobranchia: Buccinidae). J. Exp. Mar. Biol. Ecol. 69: 217-241.

Rowley, R.J. 1989. Settlement and recruitment of sea urchins (*Strongylocentrotus* sp.) in a sea-urchin barren ground and in a kelp bed: are populations regulated by settlement or post-settlement processes? Mar. Biol. 100: 485-494.

Sarver, D.J. 1979. Recruitment and juvenile survival in the sea hare *Aplysia juliana* (Gastropoda: Opisthobranchia). Mar. Biol. 54: 353-361.

Smith, K.N. & W.F. Herrnkind. 1992. Predation on early juvenile spiny lobsters *Panulirus argus* (Latreille): influence of size and shelter. J. Exp. Mar. Biol. Ecol. 157: 3-18.

Sokal, R.R. & F.J. Rohlf. 1981. Biometry. W.H. Freeman & Co., New York, NY, second edition, 859 pp.

Spight, T.M. 1975. On a snail's chances of becoming a year old. Oikos. 26: 9-14.

Spight, T.M. 1976. Ecology of hatching size for marine snails. Oecologia. 24: 283-294.

Spight, T.M. 1982. Population sizes of two marine snails with a changing food supply. J. Exp. Mar. Biol. Ecol. 57: 195-217.

Suchanek, T.H. 1981. The role of disturbance in the evolution of life history strategies in the intertidal mussels *Mytilus edulis* and *Mytilus californianus*. Oecologia. 50: 143-152.

Thorson, G. 1966. Some factors influencing the recruitment and establishment of marine benthic communities. Neth. J. Sea Res. 3: 267-293.

Vermeij, G.J. 1972. Intraspecific shore-level size gradients in intertidal molluscs. Ecology 53: 693-700.

Vermeij, G.J. 1987. Evolution and Escalation. An Ecological History of Life. Princeton University Press, Princeton, New Jersey, USA. 527 p.

Vermeij, G.J. 1993. A Natural History of Shells. Princeton University Press, Princeton, New Jersey, USA. 207 p.

Wahle, R.A. & R.S. Steneck. 1991. Recruitment habitats and nursery grounds of the American lobster *Homarus americanus*: a demographic bottleneck? Mar. Ecol. Prog. Ser. 69: 231-243.

Wahle, R.A. & R.S. Steneck. 1992. Habitat restrictions in early benthic life: experiments on habitat selection and in situ predation with the American lobster. J. Exp. Mar. Biol. Ecol. 157: 91-114.

Werner, E.E. and J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst. 15: 393-425.

Williams, L.G., Rittschof, D., B. Brown, & M.R. Carriker. 1983. Chemotaxis of oyster drills *Urosalpinx cinerea* to competing prey odours. Biol. Bull. 164: 536-548.

Wolcott, T.G. 1973. Physiological ecology and intertidal zonation in limpets (*Acmaea*): a critical look at "limiting factors". Biol. Bull. 145: 389-422.

Wolff, T. 1978. Maximum size of lobsters (*Homarus*)(Decapoda, Nephropidae). Crustaceana. 34: 1-14.

Wood, L. 1968. Physiological and ecological aspects of prey selection by the marine gastropod *Urosalpinx cinerea* (Prosobranchia, Muricidae). Malacologia. 6: 267-320.

Young, C.M. and F.-S. Chia. 1984. Microhabitat-associated variability in survival and growth of subtidal solitary ascidians during the first 21 days after settlement. Mar. Biol. 81: 61-68.

Zimmer-Faust, R.K. 1987. Crustacean chemical perception: towards a theory on optimal chemoreception. Biol Bull. 172: 10-29.

APPENDIX 1

A method for marking small juvenile gastropods.[1]

Methods used to identify individual organisms consistently over time have been invaluable tools in ecological studies, enabling reliable assessments of time dependent parameters such as growth and mortality, and an accurate determination of their variance. These methods have proven to be particularly amenable to gastropods owing to the presence of an external shell on which marks or tags can be applied with little or no adverse effects on the animal. Marking and tagging techniques have enabled the study of several ecological parameters in adult marine gastropods, including growth (Frank, 1965; Hughes, 1972; Palmer, 1983; Gosselin and Bourget, 1989), mortality (Frank, 1965; Hughes, 1972), movements (Frank, 1965; Chapman, 1983), and foraging behaviour (Menge, 1974; Hughes et al., 1992). Small organisms, however, can pose considerable problems for individual marking (Southwood, 1978). As a result, marking and tagging methods have seldom been applied to newly hatched or recently settled juvenile marine gastropods. Several methods have been developed for simultaneously labelling large numbers of invertebrate larvae (Levin, 1990), and some of these methods may be applicable to juvenile gastropods. The usefulness of these methods, however, is limited because all animals receive the same label and, consequently, individual animals can not be recognized. To my knowledge, no method of individually marking very small juvenile marine gastropods has been documented. In fact, it is sometimes perceived that small juveniles can not be individually marked due to their small size and sensitivity (Frank, 1965; Palmer, 1990). The object of this paper is to present a simple method of marking early juvenile gastropods, which consists of applying colour codes to the shells of individuals as small as 0.9 mm in length. In addition, the present study demonstrates that the method has no adverse effects on snail growth and survival, and shows that the marks are persistent over time. The method was applied to hatchlings of a marine prosobranch gastropod, *Nucella emarginata* (=*Thais emarginata*) (Deshayes). *N. emarginata* hatch from benthic egg capsules as crawl-away juveniles measuring 0.9 to 1.8 mm from the apex to the tip of the siphonal canal (pers. obs.; Spight, 1976).

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[1] A version of this appendix has been published.
Gosselin, L.A. 1993. A method for marking small juvenile gastropods. Journal of the Marine Biological Association of the U.K. 73: 963-966.

The juvenile snails are initially placed in freshwater for 30 - 40 seconds to make them retract into their shell. This decreases their susceptibility to desiccation during the following steps. Hatchling *Nucella emarginata* can be left in freshwater several minutes without apparent effects on subsequent behaviour or survival. Excess water is then removed by blotting snails onto a wet paper towel. Blotting must be very brief (one to two seconds); if water within the shell is also absorbed the hatchling is not likely to survive the following steps. Hatchlings are then secured by gently pressing them into a thin (≈2 mm) layer of non-toxic modelling clay, aperture down. Once the shell is dry, a colour code of up to three dots of nail polish is carefully applied to each hatchling under a dissecting microscope. The nail polish is applied using a small brush trimmed down to three to five strands. Hatchlings are returned to seawater as soon as the nail polish is dry. These colour codes can then easily be read under a dissecting microscope. Six colours were used to mark *N. emarginata* hatchlings: blue, red, yellow, green, orange, and purple. For clarity, combinations with two consecutive dots of a same colour were not used. Thus, 186 different combinations of these six colours could be generated when applying up to three dots of nail polish.

In order to determine if this method had an effect on growth or survival of juvenile *Nucella emarginata*, nine hatchlings were marked within 12 hours of emerging from their egg capsules. Each individual was then measured and placed in a separate cage (size= 10 x 10 x 6 cm; 610 μm mesh) in a tank with flowing seawater. Each cage also received one unmarked hatchling from the same sample of egg capsules. Small mussels (*Mytilus* spp.) and a rock with barnacles (*Balanus glandula* Darwin and *Chthamalus dalli* Pilsbry) were added as prey. Additional prey were provided as required. The hatchlings were observed and measured regularly over a period of 365 days. An additional drop of nail polish was applied to the new shell growth of all marked hatchlings on day 71. These new marks persisted for the remainder of the experiment.

When returned to seawater after being marked, hatchlings resumed crawling within five minutes. No difference in behaviour was apparent between marked and unmarked hatchlings. Throughout the experiment, the average size of marked and unmarked snails remained closely matched (Fig. A1-1). Growth (shell length increment) of marked and unmarked individuals were not significantly different during the first 30 days or during the remainder of the 365 day period (Table A1-1). In addition, the nine pairs of snails were still alive after one year.

To determine the persistence time of the nail polish marks, three cages containing a total of 39 marked hatchlings were placed in flowing seawater in the laboratory for a period of 140 days. Three other cages, containing a total of 14 hatchlings, were attached to the substratum in the intertidal zone near the Bamfield Marine Station for the same period. All cages were initially supplied with prey, and at approximately 20 day intervals the marks were examined and the supply of prey was replenished. Under laboratory conditions, 94% of the marks were still intact after 60 days (Fig. A1-2); 46% lasted longer than 100 days. Although the marks on hatchlings placed in field cages did not last as long as those in the laboratory, 93% were still intact after 40 days (Fig. A1-2). Nail polish marks were lost when the larval shell eroded. However, remaining fragments of the colour marks allowed correct identification of the hatchlings well after large portions of the marks were lost.

This marking method, therefore, did not produce any detectable effect on growth, mortality, or behaviour of the hatchlings. In addition, nail polish possessed the advantageous properties of good adhesion, hardness, and rapid drying. Trials using ink and enamel paint were unsuccessful. The ink did not adhere well to the shell and flaked off within hours after being applied; the enamel paint required considerable drying time which resulted in high hatchling mortality.

Due to their small size and cryptic behaviour, early juvenile marine gastropods have mostly been studied under laboratory conditions (Largen, 1967; Rittschof et al., 1983; Palmer, 1990; chapter II). However, I have successfully recovered live marked

TABLE A1-1

Effects of the marking method on the growth (increase in shell length) of *N. emarginata* hatchlings. Initial shell length, measured from the tip of siphonal canal to the apex, and shell growth were obtained from nine pairs of marked and unmarked hatchlings. The ocular micrometer of a dissecting microscope (measurement error ± 0.02 mm) was used for measurements on days 0 and 30. A vernier caliper (measurement error ± 0.1 mm) was used on day 365.

	Marked	Unmarked	ANOVA	
	$\bar{x}$ ± SD	$\bar{x}$ ± SD	F	p
Initial length (mm)	1.23 ± 0.10	1.25 ± 0.07	0.34	0.58
Growth (mm):				
Days 0-30	1.27 ± 0.18	1.34 ± 0.16	0.82	0.39
Days 30-365	23.7 ± 2.8	24.6 ± 2.0	1.32	0.28

Figure A1-1. Growth of marked and unmarked *N. emarginata* hatchlings. Error bars represent standard deviations. All hatchlings were kept in flowing seawater in the laboratory with an abundant supply of food. (n = nine marked and nine unmarked hatchlings).

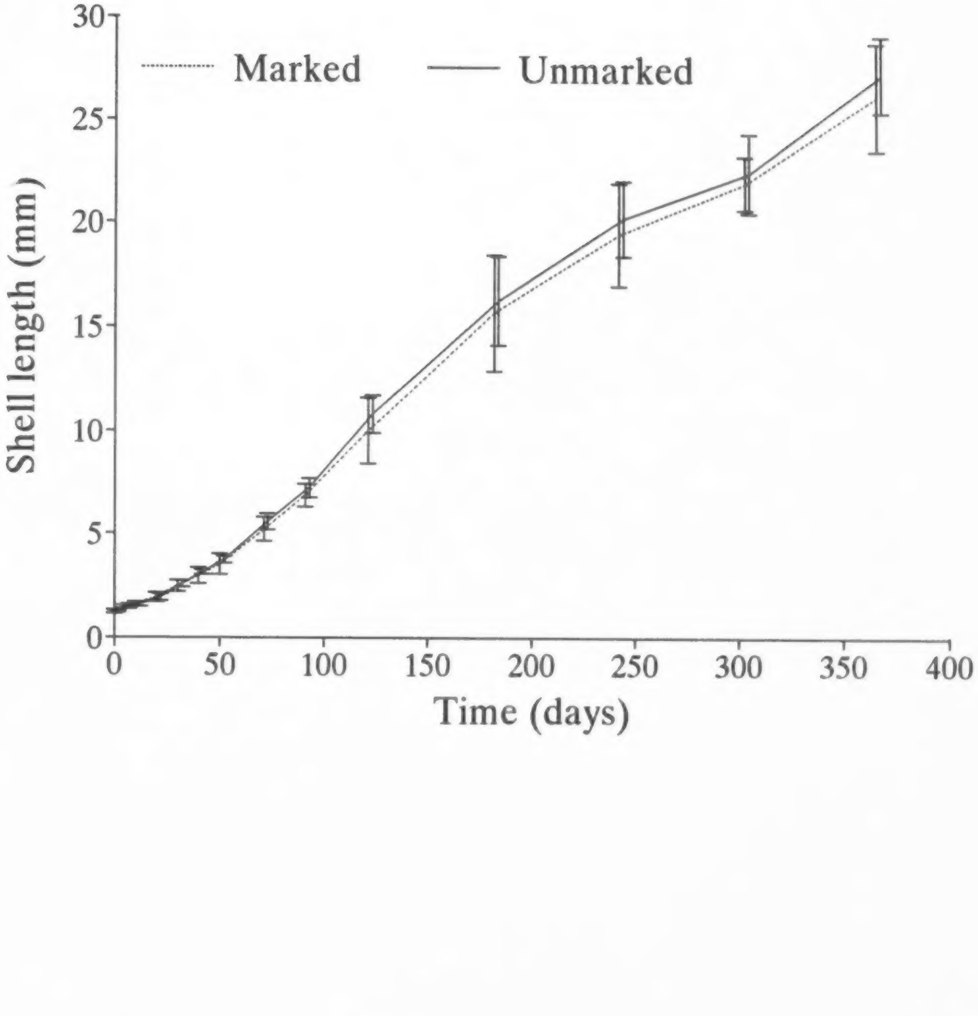
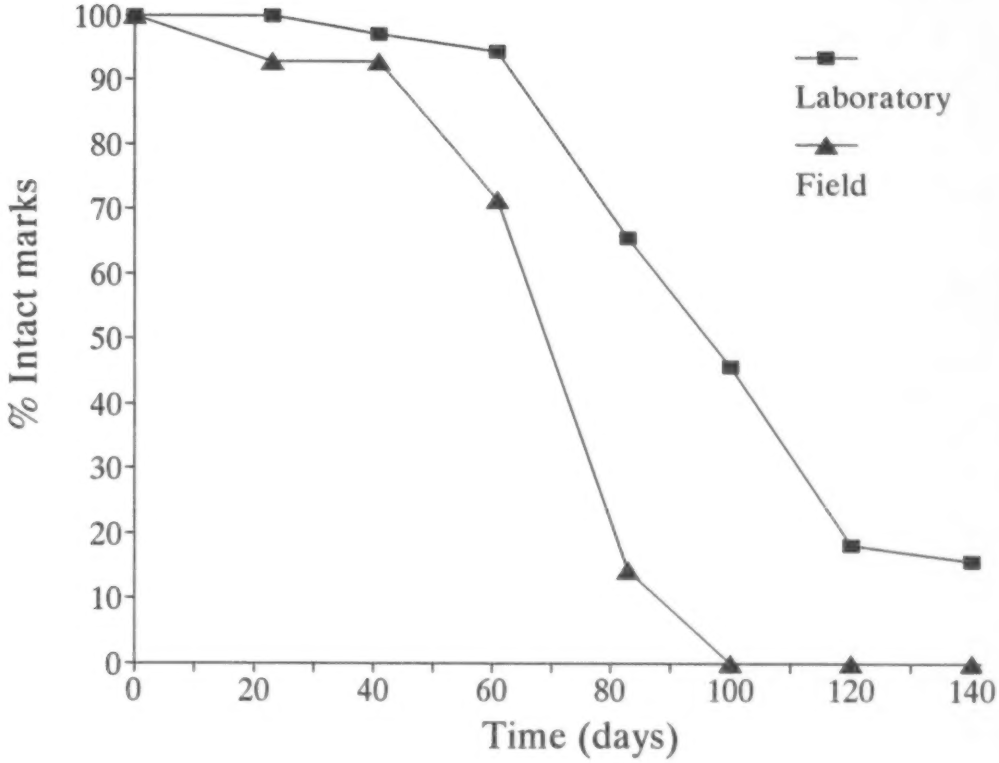

Marked
Unmarked
Shell length (mm)
30
25
20
15
10
5
0
0
50
100
150
200
250
300
350
400
Time (days)

Figure A1-2. Persistence time of marks on *N. emarginata* hatchlings. One mark per hatchling, each mark consisting of up to three dots of nail polish. "Lab." hatchlings were placed in cages in the laboratory. "Field" hatchlings were placed in cages attached in the intertidal zone. (n = 39 Lab. and 14 Field hatchlings).


100
90
80
70
60
50
40
30
20
10
0
% Intact marks
0
20
40
60
80
100
120
140
Time (days)
Laboratory
Field

Nucella emarginata hatchlings after a period of 10 days in the field (unpubl. data), demonstrating the feasibility of mark and recovery field experiments with juveniles with limited dispersal capabilities. This marking method has also been used to study growth and survival of *N. emarginata* hatchlings in relation to food type in the laboratory (chapter V). It is also likely to be effective for marking juveniles of certain bivalve species as well as other juvenile invertebrates bearing hard external structures. To date, most studies of the ecology of post-metamorphic marine invertebrates have been directed at the late juvenile and adult stages. Very little information is available on the early juvenile period of these organisms. Methods such as the one described herein will facilitate the study of very young individuals and contribute to a better understanding of the ecology of juvenile marine invertebrates.

References

Chapman, M.G. 1986. Assessment of some controls in experimental transplants of intertidal gastropods. J. Exp. Mar. Biol. Ecol. 103: 181-201.

Frank, P.W. 1965. The biodemography of an intertidal snail population. Ecology. 46: 831-844.

Gosselin, L.A. and E. Bourget. 1989. The performance of an intertidal predator *Thais lapillus*, in relation to structural heterogeneity. J. Anim. Ecol. 58: 287-303.

Hughes, R.N., M.T. Burrows, and S.E.B. Rogers. 1992. Ontogenetic changes in foraging behaviour of the dogwhelk *Nucella lapillus* (L.). J. Exp. Mar. Biol. Ecol. 155: 199-212.

Largen, M.L. 1967. The diet of the dog-whelk, *Nucella lapillus* (Gastropoda Prosobranchia). J. Zool. (Lond.). 151: 123-127.

Levin, L.A. 1990. A review of methods for labelling and tracking marine invertebrate larvae. Ophelia. 32: 115-144.

Menge, J.L. 1974. Prey selection and foraging period of the predaceous rocky intertidal snail, *Acanthina punctulata*. Oecologia. 17: 293-316.

Palmer, A.R. 1983. Growth rate as a measure of food value in thaidid gastropods: assumptions and implications for prey morphology and distribution. J. Exp. Mar Biol. Ecol. 73: 95-124.

Palmer, A.R. 1990. Predator size, prey size, and the scaling of vulnerability: hatchling gastropods Vs. barnacles. Ecology. 71: 759-775.

Rittschof, D., L.G. Williams, B. Brown, and M.R. Carriker. 1983. Chemical attraction of newly hatched oyster drills. Biol. Bull. 164: 493-505.

Southwood, T.R.E. 1978. Marking invertebrates. In: Animal Marking. Recognition Marking of Animals in Research. Ed. B. Stonehouse, University Park Press Baltimore, USA. pp. 102-106.

Spight, T.M. 1976. Hatching size and the distribution of nurse eggs among prosobranch embryos. Biol. Bull. 150: 491-499.

APPENDIX 2

Seasonality of spawning, hatching, and capsular mortality in *Nucella emarginata.*

Females of the marine prosobranch gastropod *Nucella emarginata* (northern)(cf. Palmer et al., 1990) on Washington and Oregon coasts are reported to produce benthic egg capsules throughout the year, but most abundantly in the winter and spring (Seavy, 1977 [cited by Strathmann, 1987]; Spight, 1982). In Barkley Sound, British Columbia, however, spawning during the period May 1990 to February 1991 was observed mainly in the late spring and throughout the summer (pers. obs.). By late October 1990, egg capsule production had ceased at virtually all sites. Inspections of the shore once or twice a month from November 1990 to early March 1991 revealed no new egg capsules.

Given the marked divergence between these observations and the published information on spawning season in *N. emarginata*, the present study of egg capsule production was undertaken in order to document the seasonality of spawning by this abundant rocky intertidal gastropod in Barkley Sound. In addition, since little is known of the fate of these egg capsules and their contents (but see Rawlings, 1990), this study also documents the numbers of egg capsules from which live offspring emerged as well as those in which the contents were destroyed by predators or died of other causes. The present appendix therefore briefly presents the methods and results of this field study.

This study was initiated on 20 March 1991, approximately two weeks after a few new egg capsules had first been observed in the field. Observations were then carried out fortnightly until 4 June 1992, and monthly thereafter up to the conclusion of the study on 13 November 1993. For the period of January to April of 1992 and 1993, however, only one set of observations was made in mid-February. Few egg capsules were being produced when the study was terminated.

Snails and egg capsules were abundant during the summer of 1990, the year before the study was initiated, at each of the three selected sites: Ross Islets (48°52'35" N, 125°09'65" W), Dixon Island (48°51'15"N, 125°06'90"W), and Kirby Point (48°50'85"N, 125°12'40"W). Each observation area consisted of an undisturbed vertical rock wall, and included bare rock, small clusters of mussels (*Mytilus californianus* and *M. trossulus*), barnacles (*Balanus glandula*, *Chthamalus dalli*, and *Semibalanus cariosus*), fucoid algae (*Pelvetiopsis limitata* and *Fucus* spp.) and filamentous algae (mainly *Cladophora columbiana*). Algae, however, were mostly absent from the observation area at Kirby Point. Details of each observation area are listed in Table A2-1.

During inspections, each egg capsule was individually examined and its status was recorded as follows: *intact*: healthy egg capsules with developing embryos; *hatched*: unplugged capsules from which fully metamorphosed snails were hatching or had hatched; *damaged*: capsules that had been ruptured or partly eaten by predators, as evidenced by distinctive perforations or bite-marks left by the predators on the capsule walls (cf. Rawlings, 1990); *dead*: egg capsules with no apparent damage but in which the embryos were visibly dead, as evidenced by a pink or purple colour, or by weak capsule walls and white, fine-textured contents. Once recorded, hatched, damaged, and dead capsules were then removed from the substratum. The abundance of adult snails at the study sites was not monitored.

The above method did involve a certain measure of subjectivity. Embryo mortality may not always be apparent shortly after death, and therefore non-predation mortality may not have been recorded on the first observation after death occurred. In addition, capsules in which the contents had hatched or died a few weeks before the time of an observation could not always be identified with certainty, and some small punctures produced by predators (Rawlings, 1990) may have been overlooked. The following results for hatched, damaged, and dead capsules must therefore be considered as approximate values.

One last point must be addressed regarding the sampling design. When starting the study, the possibility of using several small quadrats rather that one large area at each site was considered, but preference was given to the latter. The study areas had to be selected as being likely to receive egg capsules whenever the females were spawning. In small areas, however, the availability of spaces in which the snails could spawn

TABLE A2-1

Characteristics of the three observation areas in which the production and fate of *Nucella emarginata* egg capsules were monitored during this study.

	Ross Islet	Dixon Island	Kirby Point
Wave exposure	Protected	Moderate-protected	Exposed
Surface area	3.53 m^2	6.11 m^2	8.95 m^2
Maximum height	0.99 m	1.47 m	1.50 m
Minimum height	0.18 m	0.62 m	0.10 m
Width	7.76 m	6.64 m	10.9 m

changed considerably from year to year, and even over a period of a few months. Areas of 1 m^2 or less that had many adequate spaces at the start of the study were then often overgrown by mussels or filamentous algae, or were completely cleared to bare rock during winter storms. The use of quadrats would have produced results with considerable variability reflecting small scale changes in availability of spawning spaces rather than actual egg capsule production by the population. The observation areas used in this study were sufficiently large that while adequate spaces for spawning disappeared in some parts, new spaces were produced in other parts. Consequently, there were always abundant snails and adequate spaces for spawning within these areas. Single large areas were also easier to repeatedly locate with accuracy over long periods of time without the use of markers, which might produce some disturbance.

Spawning varied considerably from year to year. At each site, the annual production of egg capsules varied two- to threefold (Table A2-2). The largest production of egg capsules, however, occurred on a different year at each site, suggesting that total capsule production may have depended more on the recent history of the snail population and local conditions (e.g. availability of food and population density) than on weather and seawater temperature.

Spawning also peaked at a slightly different time each year. This was most apparent at Ross Islets (Fig. A2-1a) and Kirby Point (Fig. A2-3a). Changes in the peak and duration of spawning may have been related to seawater temperatures, which warmed up earlier and reached higher levels in 1992 and 1993 due to the El Niño (Fig. A2-1b, A2-2b, A2-3b). Overall, however, most spawning occurred from early April to late August, with few capsules produced during the winter (Fig. A2-1a, A2-2a, and A2-3a).

Most hatching occurred from May to September (Fig. A2-4), although the time of peak hatching varied according to the time of peak spawning. Few snails hatched during the fall, and almost none of the capsules present in the late fall or winter produced live hatchlings. The proportion of capsules in which the contents were destroyed by predation was generally constant throughout the year, and mostly remained below 0.5% / day

TABLE A2-2

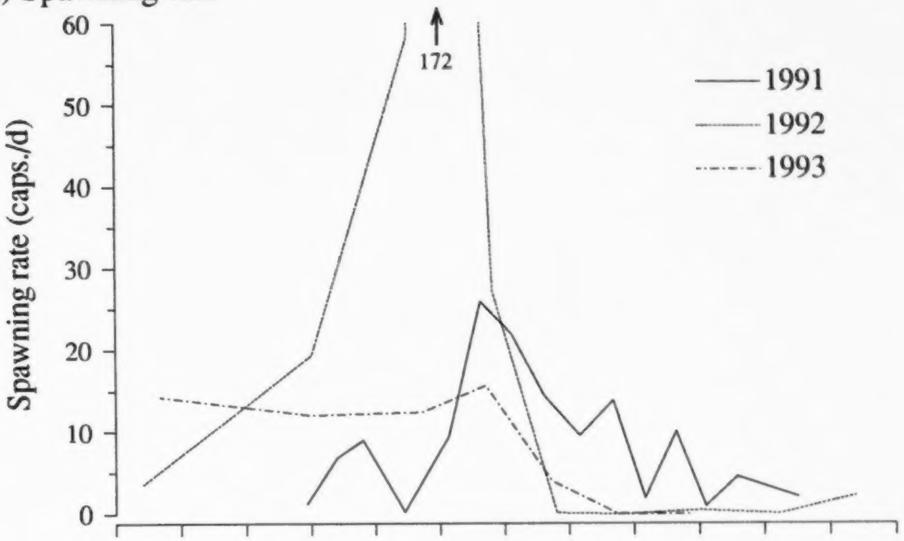
Total number of egg capsules spawned by *Nucella emarginata* within the observation areas for each year of the study.

Year	Ross Islet	Dixon Island	Kirby Point
1991	1842	1079	1239
1992	6197	2758	888
1993	2859	3364	556

Figure A2-1. Egg capsule production by *Nucella emarginata* and surface seawater temperatures at Ross Islets from March 1991 to November 1993. a) Number of capsules spawned per day in the observation area, each value plotted on the median day of the observation period. b) Surface seawater temperature measured 10 - 30 m from the shore at a depth of 10 - 30 cm.

Ross Islets

a) Spawning rate



b) Seawater temperature

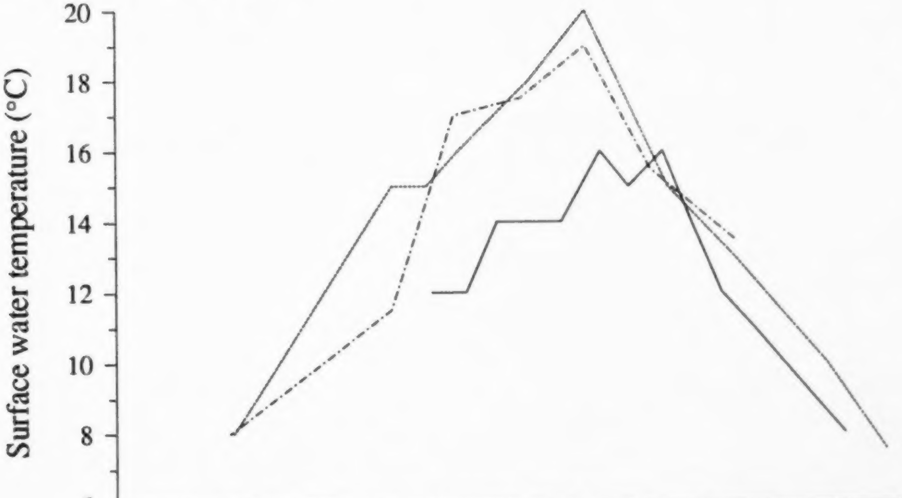
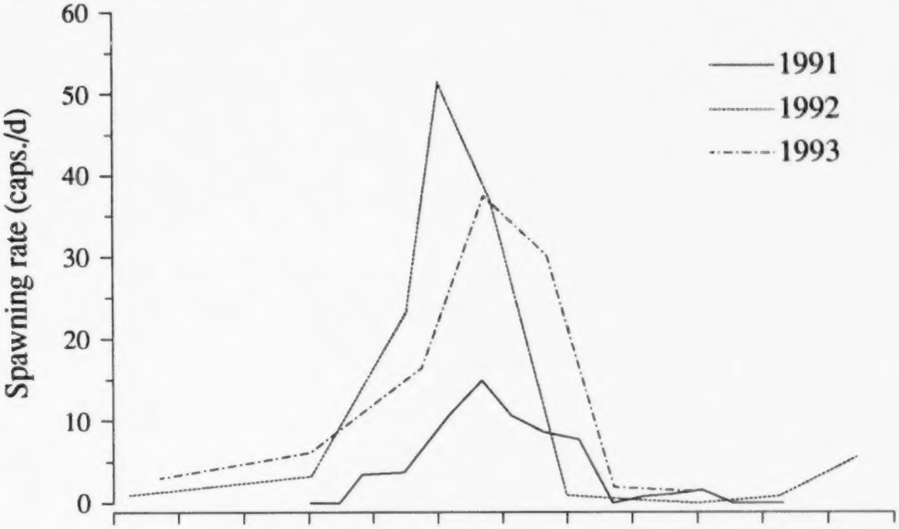


Figure A2-2. Egg capsule production by *Nucella emarginata* and surface seawater temperatures at Dixon Island from March 1991 to November 1993. a) Number of capsules spawned per day in the observation area, each value plotted on the median day of the observation period. b) Surface seawater temperature measured 10 - 30 m from the shore at a depth of 10 - 25 cm.

Dixon Island

a) Spawning rate



b) Seawater temperature

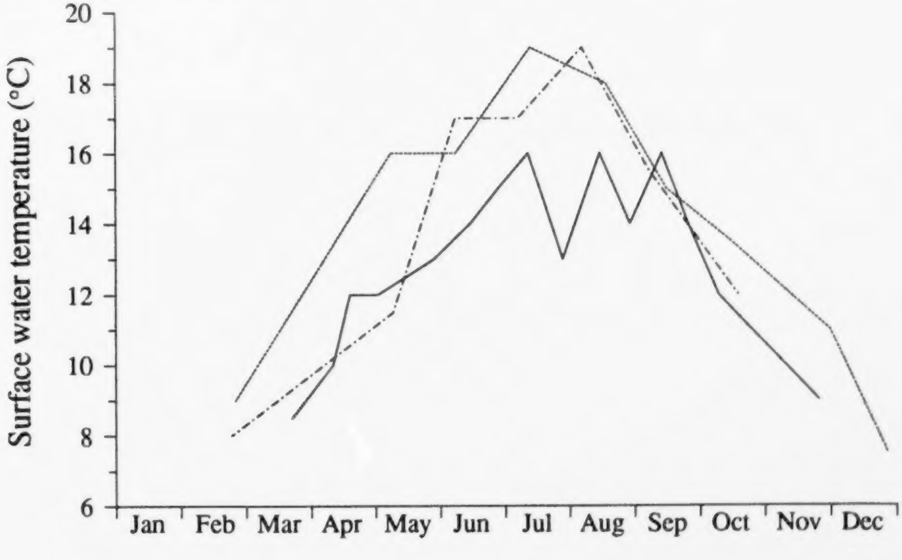
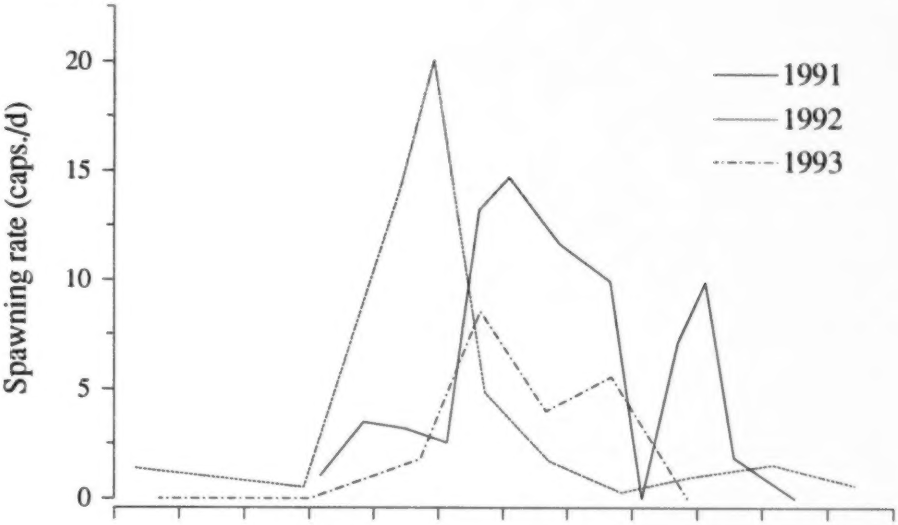


Figure A2-3. Egg capsule production by *Nucella emarginata* and surface seawater temperatures at Kirby Point from March 1991 to November 1993. a) Number of capsules spawned per day in the observation area, each value plotted on the median day of the observation period. b) Surface seawater temperature measured 10 - 30 m from the shore at a depth of 10 - 25 cm.

Kirby Point

a) Spawning rate



b) Seawater temperature

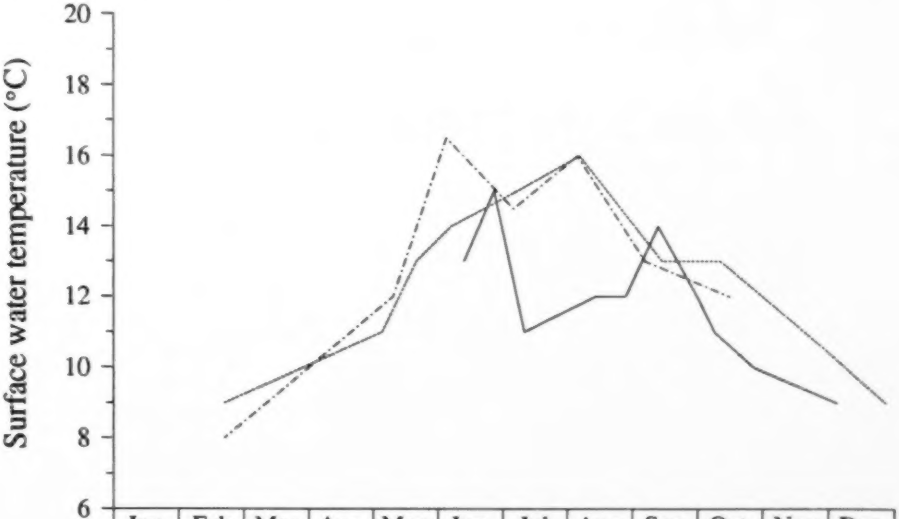
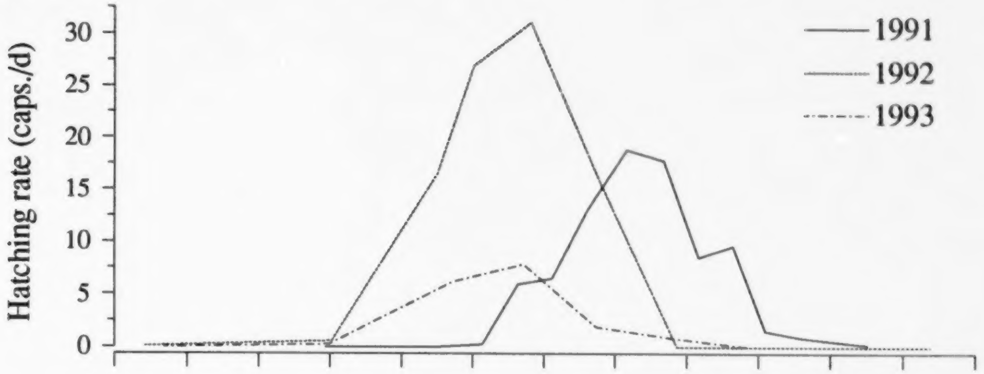


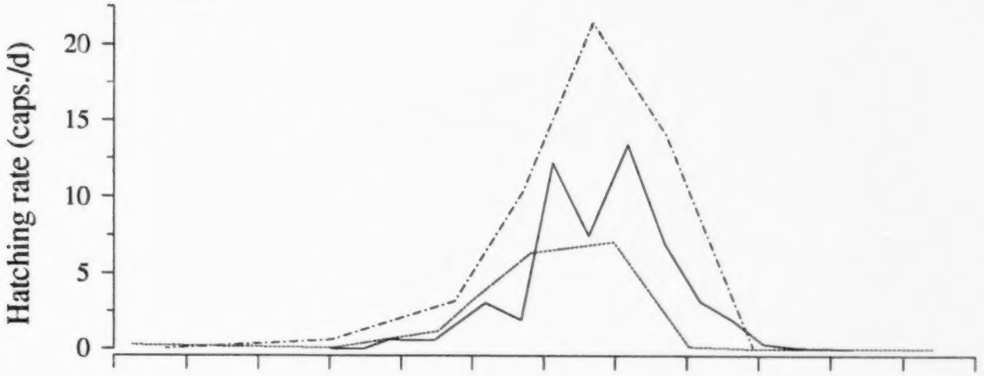
Figure A2-4. Rate of hatching (based on counts of "hatched" capsules, per day) through the year within observation areas at each site. Each value plotted on the median day of the observation period.

Hatching rate

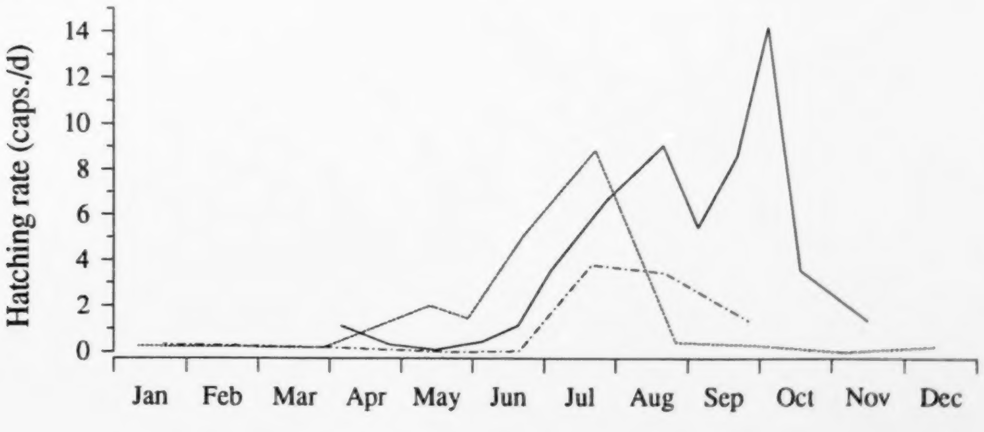
a) Ross Islets



b) Dixon Island



c) Kirby Point



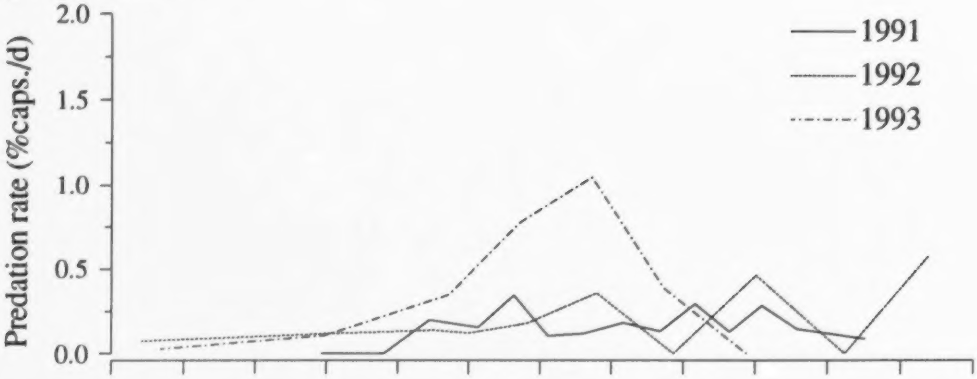
(Fig. A2-5). Capsular mortality due to factors other than predation, however, was consistently higher than predation mortality, and increased throughout the summer to reach maximum mortality rates from late July through to September (Fig. A2-6). This trend may in part be an artifact, however, of the decreasing proportion of newly spawned capsules in the field late in the summer.

The likelihood that egg capsules would produce viable offspring varied considerably among years. At all sites, the proportion of capsules in which embryos developed through to hatching was higher in 1991 than in the following two years (Fig. A2-7a). Total predation mortality (Fig. A2-7b) varied little among years, however, and did not appear to be the main cause of decreased survivorship in 1992 and 1993. Mortality due to factors other than predation (Fig. A2-7c), which increased after 1991, appears to be the main reason for the reduced number of hatched capsules in these years. The first year of the study was the coolest of the three years (Fig. A2-1b, A2-2b, A2-3b); the subsequent warmer seawater temperatures in 1992 and 1993 may have affected the metabolism of the embryos or of the spawning females, or been conducive to conditions favouring protozoan infections or diseases. A reduced fertilization rate might also be partly responsible for the higher "mortality" rates in late summer and fall, and in years 1992 and 1993.

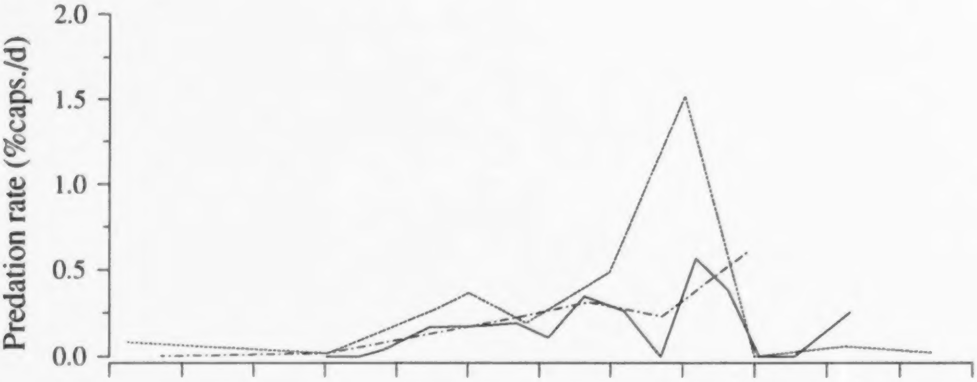
Figure A2-5. Seasonal rate of capsular mortality due to predation (based on counts of "damaged" capsules relative to the total number of capsules present in the observation area during the previous interval) within observation areas at each site. Each value, plotted on the median day of the observation period.

Predation mortality rate

a) Ross Islets



b) Dixon Island



c) Kirby Point

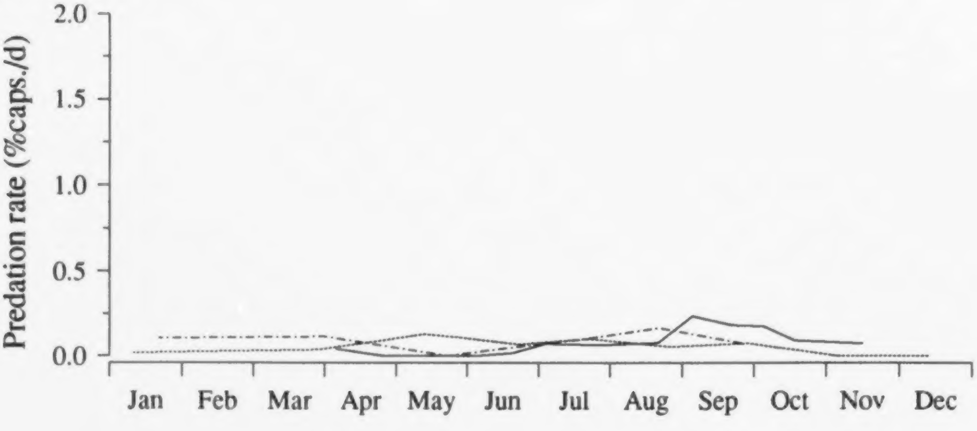
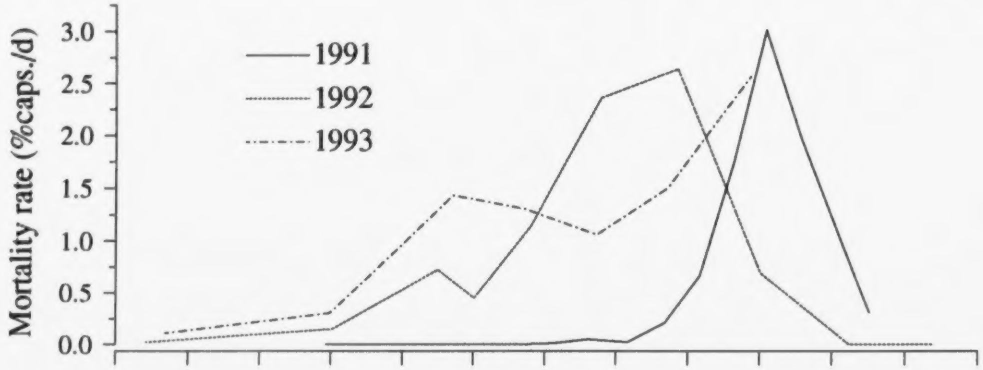


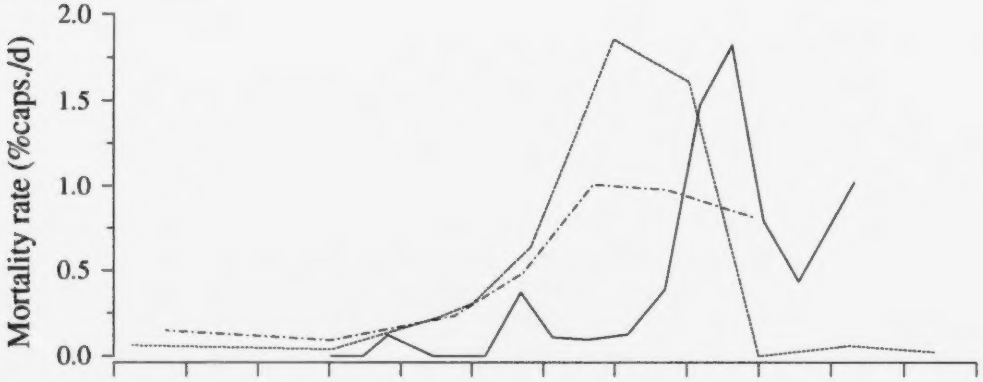
Figure A2-6. Seasonal rate of capsular mortality due to causes other than predation (based on counts of "dead" capsules relative to the total number of capsules present in the observation area during the previous interval) throughout the year within observation areas at each site. Each value plotted on the median day of the observation period.

Non-predation mortality rate

a) Ross Islets



b) Dixon Island



c) Kirby Point

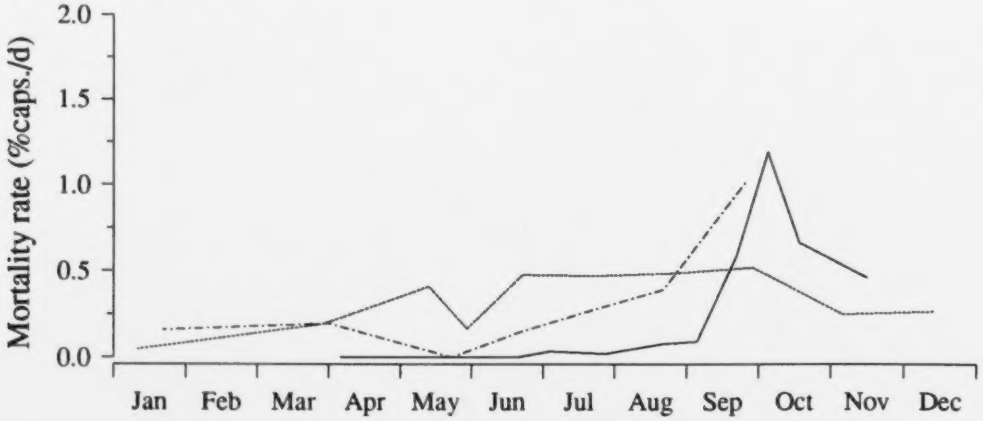
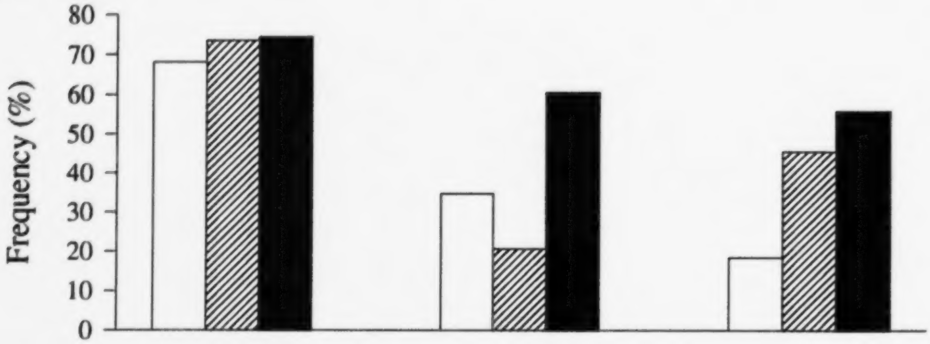


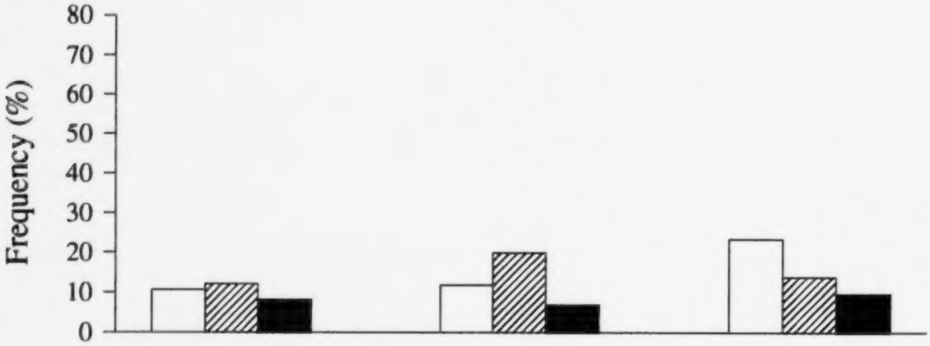
Figure A2-7. Fate of egg capsules spawned by *Nucella emarginata* within observation areas at Ross Islets, Dixon Island, and Kirby Point for each year of the study. Percentages calculated relative to the total number of egg capsules produced that year (Table A2-1).

Fate of egg capsules

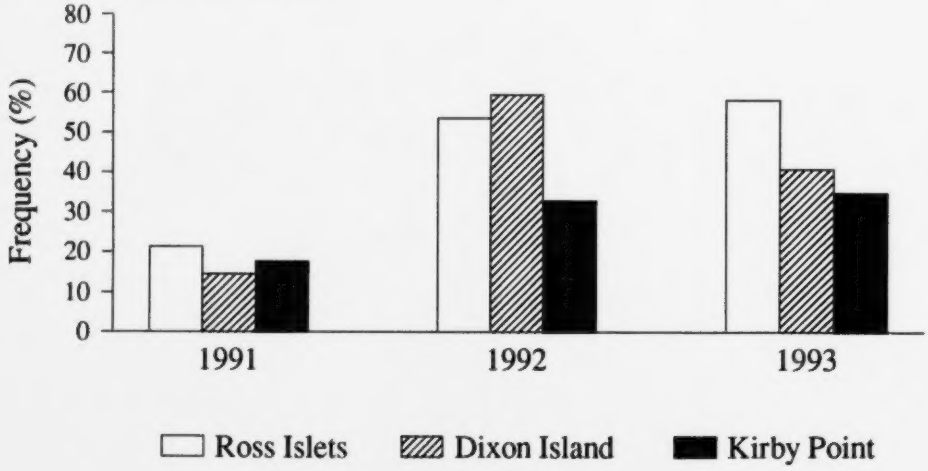
a) Hatched



b) Predation mortality



c) Non-predation mortality



References

Rawlings, T.A. 1990. Associations between egg capsule morphology and predation among populations of the marine gastropod, *Nucella emarginata*. Biol. Bull. 179: 312-325.

Seavy, D.K. 1977. Seasonal Gametogenesis and Egg Laying in the Prosobranch Gastropods *Nucella lamellosa*, *Nucella emarginata*, *Searlesia dira*, and *Amphissa columbiana* on the Oregon Coast. Ph.D. Diss., Oregon State Univ., Corvallis. 179pp.

Spight, T.M. 1982. Population sizes of two marine snails with a changing food supply. J. Exp. Mar. Biol. Ecol. 57: 195-217.

Strathmann, M.F. 1987. Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast. Univ. of Washington Press, Seattle, Wash. 670 pp.